

GROWTH AND DEVELOPMENT OF CITRUS ROOTS  
IN RELATION TO SEASON, ROOTSTOCK, SHOOT  
GROWTH, AND ENVIRONMENTAL FACTORS

BY

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The seasonal pattern of root growth of young 'Valencia' orange trees on rough lemon and Carrizo citrange rootstocks was studied in relation to shoot growth, soil temperature, and soil water stress in root observation chambers containing a reconstituted profile of a fine sand orchard soil. The chambers were installed below ground at a field site and were periodically raised above ground to record root growth. Entire root systems were recovered from the chambers to study the morphological development of the root system. The effect of exposure to light on root growth was investigated in Carrizo citrange.

Under the subtropical climatic conditions of central Florida, root growth occurred from February to early December. The overall seasonal trend in root growth was significantly correlated with soil temperature. The most intense

root growth activity occurred during summer, when soil temperatures were above 27°C. Throughout the year, a marked alternation of peak periods of root and shoot growth activity was observed. Root growth activity declined with the initiation of each shoot growth flush and then increased immediately following the cessation of shoot elongation. The decline in activity was largely due to the reduced development of higher order laterals. There were no differences between rootstocks in the seasonal pattern of root growth.

The number of growing roots and rate of elongation were markedly reduced at a soil water tension of 0.5 bar. Brief periods of water stress had no effects on the subsequent pattern of root growth after rewatering.

Individual roots underwent cycles of extension growth. The duration of growth cycles and elongation rates decreased with successive orders of branching. Replacement roots arising from the ends of taproots and main laterals severed during digging from the nursery were largely responsible for the rapid expansion of the root system and increased the extent of branching. During the first year after transplanting the total length of fibrous roots increased from 150 m to more than 3,000 m. Fibrous roots comprised more than 98% of the total length of the root system.

Continuous exposure to light suppressed the development of lateral roots. Brief exposure caused less reduction in lateral root development.

## INTRODUCTION

The root systems of woody perennials are comprised of several different types of roots which vary in their pattern of development and life history. Detailed information on the growth behavior and life history of individual roots, as well as on the morphological development of the root system is available only for a few tree crops (6, 8, 66, 69, 71, 86, 110, 112, 137, 138). No detailed studies have been carried out on the morphological development of the root system of citrus trees and the growth dynamics of citrus roots has received relatively little attention. This lack of information reflects the considerable technical difficulties involved in excavating entire tree root systems from the soil and in observing root growth under field conditions.

Information on the growth dynamics and morphological development of the root system is important for several reasons. The rate at which the root system extends into new areas of soil depends on the rate of growth of pioneer roots, while the pattern of development of fine lateral roots determines the efficiency with which the soil volume is exploited (5, 9, 36, 94, 114, 127, 139). New extension growth is considered to be especially important for the uptake of nutrients which diffuse slowly in soils (36) and

for water uptake in partially wetted soils, where water movement to the surface of the root by capillary conductivity is low (22). In perennial crops, new root growth replaces old roots that are no longer functional and allows the root system to adapt to changing environmental conditions (5). A greater understanding of the factors that affect the pattern of root growth and of the relationship of rooting characteristics to tree performance will lead to the development of more efficient irrigation, fertilization, and soil management practices, and will allow better use to be made of inherent differences in root growth behavior that exist between fruit tree rootstocks.

The objectives of this study were (a) to study the seasonal periodicity of root growth of young citrus trees in relation to soil temperature, soil water tension, rootstock, and shoot growth; (b) to make detailed observations on the growth behavior of different types of roots; and (c) to study the morphological development of the root system.



## LITERATURE REVIEW

Root growth characteristics of trees vary with species and are greatly influenced by the soil environment and certain cultural practices (5, 82, 87). Fruit trees, unlike forest and ornamental species, are propagated commercially by budding or grafting on selected rootstocks. Thus, the form of the fruit tree root system depends not only on growing conditions but also on the choice of rootstock.

### Form and Development of the Citrus Root System

#### Morphology

The root system of mature citrus trees consists of an extensive, well-branched framework of woody lateral roots bearing bunches of fine fibrous roots. Differences between rootstocks have been found in the configuration of the woody framework, the extent and depth of rooting, and in the distribution and concentration of the fine fibrous roots (31, 33, 48, 116, 132).

The root system arises by elongation and branching of the primary root, which is derived from the root pole of the embryo (44). If not impeded in its vertical growth the primary root develops into the taproot. Although a

prominent taproot is evident in seedlings and nursery trees (33, 116), a well-differentiated taproot is not always evident in mature trees (15, 60, 132), and the taproot serves primarily as a source of laterals. Webber (132) reported that sweet orange and rough lemon commonly exhibited no taproot, whereas calamondin and sour orange had one or more well-developed taproots which grew to considerable depth. Cutting back the taproot during transplanting induced branching and multiple taproot development.

The bulk of the woody framework of the root system is derived from major lateral roots which develop from the primary root and radiate out from the trunk in all directions. Lateral roots responsible for the rapid expansion of the root system into new areas of soil are termed "pioneer" roots (118). These roots are characterized by a large (1-2 mm) tip diameter and are capable of undergoing copious secondary thickening. Lateral roots occur along the pioneer roots and many of these laterals undergo extensive branching to form bunches of fine fibrous roots. Less frequently new main laterals arise, and some of these roots undergo considerable secondary thickening and become part of the woody framework of the root system. Although no quantitative data are available, differences between citrus rootstocks in the abundance of major laterals radiating out from the trunk have been observed (33, 116).

The origin of woody roots in tree root systems is unresolved (139). There is no clear indication that the

original laterals which develop acropetally behind the tip of the primary root become the major woody laterals of the mature root system. In red maple, Lyford and Wilson (86) considered that the initial major laterals developed only from adventitious primordia from the basal region of the primary root. Branching of major laterals occurs infrequently. It is not known if these woody lateral branches develop from different primordia or from the same type of primordia as non-woody roots but follow a different pattern of development. New laterals have been observed to arise adventitiously from the older woody regions of apple root systems in underground observation laboratories (110). Whether these roots arise from primordia formed de novo or from dormant primordia differentiated earlier is not known.

With citrus, roots less than 1.5 mm in diameter are classified as fibrous roots. The fine fibrous roots occur in bunches 20 to 30 cm long and grow out in all directions from the woody framework of the root system. Root size decreases with each order of branching, and the diameter of the smallest roots is less than 0.5 mm. Some secondary vascular tissue is formed in the main root of the fibrous root bunches, but little or none occurs in the finest roots (118). Differences between rootstocks in the morphology of the fibrous root bunches were observed by Castle and Youtsey (33). Fibrous roots of sweet orange, Carrizo citrange, and especially Swingle citrumelo were less

branched than the fibrous roots of other rootstocks. Atkinson et al. (6) found with apple rootstocks that roots less than 2 mm in diameter contributed little to total dry weight and volume of the root system, but accounted for 42 to 52% of the total root surface area and 78 and 81% of the total root length. The study further showed that the relative distribution of different sized roots varied with depth and depended on the root parameter measured. No comparable data are available for citrus.

#### Root Distribution and Density

Depth of rooting in citrus depends on tree age, rootstock, and the nature of the soil profile. With the exception of vigorous rootstocks growing on deep sandy soils in Florida, the bulk of the root system is usually located in the top 60 to 75 cm of soil (15, 18, 30, 79, 124). On deep sands in Florida, roots have been detected below 5 m (48). The root system extends laterally well beyond the width of the canopy. In high density plantings the root systems of adjacent trees soon overlap (15). Citrus roots have been detected up to 14 m from the trunk in 44 year old rough lemon (53).

Citrus fibrous roots are typically most abundant near the surface and decrease in concentration with depth and distance from the trunk (11, 20, 21, 30, 48, 92). Reported values of fibrous root density near the surface range from 0.4 to 11.8 g/dm<sup>3</sup>, and vary greatly with rootstock and soil

conditions (21, 23, 30, 48, 74, 104). There is only one report of root length density in citrus (91). Values ranged from 23 to 52 dm/dm<sup>3</sup> and are considerably higher than values reported for some deciduous fruit trees (5).

Based on depth of rooting and the distribution of fibrous roots within the root zone, under conditions allowing unrestricted development, Castle and Krezdorn (31) recognized two general types of citrus root system: extensive and intensive. The former type of root system was characterized by extensive lateral and vertical development, and more than 50% of the fibrous roots were located below 76 cm. Rootstocks with an intensive type of root system had a similar total root weight, but more than 60% of the fibrous roots were above 76 cm. Some rootstocks appeared to be intermediate in type, but in most cases had characteristics more similar to one of the general types. Rough lemon was typical of the extensive type of root system and trifoliate orange was typical of the intensive type.

#### Modification by Soil Type and Cultural Practices

The form and extent of the citrus root system are modified by the physical and chemical characteristics of the soil profile. On deep fine sands in Florida, Ford (48) found root development to a depth of 5.2 m, and Castle and Krezdorn (31) reported mean depths of rooting from 2.1 to 3.7 m for a range of rootstocks. In contrast, on sandy loam soils a much shallower root system develops and

root growth below 1.5 m is apparently sparse (2, 15, 18, 19, 20, 79). On a fine sandy loam in California, Boswell et al. (15) found that 90% of the woody framework was confined to a depth of 76 cm and no roots greater than 1.5 mm in diameter occurred below 91 cm. On deep sands the concentration of fibrous roots often declines sharply below the surface 13 to 25 cm (30, 48), whereas on loams a more gradual decline in fibrous root concentration with depth has been observed (11, 20, 79).

In addition to root distribution, studies with apples indicate that root appearance and branching may also be affected by soil texture (98, 115). In sand, apple roots were found to be long, thin, straight and spreading, whereas in heavier soils roots were short, tapering and highly branched.

The principle profile characteristics that impede vertical development of the root system are poor drainage and a compacted or poorly aerated horizon. Reitz and Long (104) found a significant correlation between the average depth of the water table and the depth to include 75% of the root system. The maximum depth of rooting was less than 1 m. Minessy et al. (92) also observed that the lateral spread of the root system was reduced with high water tables. Root death under water-logged conditions results from poor aeration, and the formation of sulphides and nitrites by reducing bacteria (52). Enhanced fibrous root growth above the water table in fine sandy soils has been

observed in situations where the height of the water table was stabilized by tile drains (49).

Citrus root growth is restricted by subsoil clay. Ford (50) detected no growth where the clay content exceeded 28%. In clay soils an air content of 9 to 10% at field capacity is apparently critical (99, 142). The presence of a lime or marl horizon (124), a subsoil pH below 4.6 to 5.0 (54), and high levels of metals (copper, zinc, manganese) (54, 56, 120) have also been found to restrict root growth.

Several cultural practices affect the distribution and density of citrus fibrous roots. High rates of nitrogen (55, 122) and phosphate (121) fertilizers have been associated with reductions in fibrous root density to a depth of 152 cm. Cahoon et al. (20) found that distribution with depth and the total quantity of roots in the top 122 cm depended on the type of nitrogen fertilizer. Urea and ammonium sulphate produced the highest quantity of roots and manure the least. Smith (122) also observed an effect of the source of nitrogen and an effect of placement. Sodium nitrate resulted in a significant reduction in the quantity of fibrous roots in the top 152 cm compared to ammonium nitrate and anhydrous ammonia. Injection of anhydrous ammonia in a 4.5 m swath increased root concentration in the fertilized zone, but there was a concomitant decrease in the unfertilized zone. Although fertilizer practices can influence root growth to a considerable depth, the largest effects generally occur near the surface.

Cahoon et al. (20) considered that fertilizers influenced root growth indirectly by changing soil characteristics such as water infiltration rate, pH, and salinity.

The total quantity, lateral distribution, and proportion of fibrous roots at depth are influenced by the method of irrigation (11, 12, 19, 79, 109, 124). Atkinson (5) concluded after reviewing the effects of irrigation on root growth of fruit trees that specific systems interact with growing conditions and climate to affect response. The largest effects have occurred with the recent introduction of irrigation systems that wet a limited volume of soil. With trickle or drip irrigation systems, where only 30 to 40% of the soil volume is wetted, the highest concentration of fibrous roots occurs around the emitters (11, 109). In young orchards, the limited wetted volume results in a restricted root zone and the development of high root densities within the irrigated area (12).

The use of herbicides is widespread in citriculture. As well as providing weed control, the use of herbicides reduces the adverse effects of tillage on soil structure and increases soil permeability to water (75). Kimball et al. (79) reported that changing from tillage and furrow irrigation to non-tillage and sprinkler irrigation resulted in a higher total quantity of roots in the top 150 cm and a substantially higher proportion of roots in the surface 25 cm. In Australia, Cary and Evans (26) found root growth to within 1 cm of the surface in non-tilled herbicide plots,



whereas in tilled plots roots were confined to below the depth (10 cm) of normal cultivation. Improved root growth has also been achieved with the incorporation of soil amendments in the profile. Calvert et al. (23) found a higher total quantity of roots and a higher proportion at depth where the soil had been deep tilled to a depth of 105 cm and a heavy application of limestone mixed with the soil prior to planting. The soil type was a sand with a highly impermeable spodic horizon at 86 to 107 cm. The improved root growth was apparently due to the more favorable pH for growth in the lower soil layers, the increased concentration of available calcium, and an increase in the rate of nitrification.

The influence of tree spacing on the development of the root system of 'Washington' navel orange trees on Troyer citrange was studied in California by Kaufmann et al. (78) and Boswell et al. (15). Root spread ranged from 6.1 m for trees planted at 6.7 x 6.7 m to 3.5 m for trees planted at 2.7 x 4.6 m. At close spacing the root systems of adjacent trees overlapped, and for much of the profile fibrous root density was apparently near maximum for the conditions of the experiment. Trees at wider spacings had fewer fibrous roots. Spacing did not affect the number of main laterals per tree, but root diameter decreased with closer spacing. Higher root densities at closer spacings were also observed with 'Pineapple' orange trees on rough lemon in Florida (30). The effect of spacing, however, was

not independent of sampling depth. At the closest spacing, the density of fibrous roots increased between 32 and 96 cm before gradually decreasing with depth, as occurred at the wider spacings. The significance of increased root density at depth with closer tree spacings in the utilization of soil resources has been discussed by Atkinson (4).

### Development and Life History of Individual Roots

#### Primary Growth

The term root tip is generally used in a broad sense to include the apical meristem and the subadjacent primary meristematic tissues (44). In roots the apical meristem is sub-terminal, being covered by a protective rootcap. As the root is pushed through the soil by the division and expansion of cells behind the apex, the rootcap changes shape and its outer cells slough off (109).

In citrus, the vascular cylinder (or stele), the cortex, and the rootcap are each derived from independent layers of cells in the apical meristem, with the epidermis differentiating from cells having a common origin with the rootcap cells (65, 118). The transition from apical meristem to mature primary body occurs gradually. Different cell types differentiate at different distances behind the apex and consequently the regions of cell division, enlargement, and differentiation overlap.

Vascularization in citrus roots follows the usual pattern (44, 65, 118). Differentiation and maturation of the

phloem and xylem occur acropetally, and the first phloem elements mature closer to the apex than the first xylem elements. The first protoxylem elements form on radii which alternate with the strands of primary phloem. The number of protoxylem poles ranges from 7 to 9 in the primary root, 4 to 6 in the larger lateral roots, down to 2 in the smallest roots. The protoxylem matures behind the region of elongation.

No data are available for citrus on the distance behind the apex at which differentiation and maturation of the various tissues occur. In pear roots, Esau (43) found that the regions of phloem and xylem formation were first delimited 0.2 to 0.3 mm from the apex. At 0.6 to 0.7 mm the first sieve tube elements differentiated, whereas the deposition of secondary walls in the first xylem elements was not initiated until some 5 mm from the apex. The proximity of mature vascular elements to the apical meristem depends on the rate of elongation, which varies with root type and environmental conditions (95, 108). In rapidly elongating roots mature vascular elements occur farther from the apex.

The endodermis is typically a single layer of cells which differentiates from the innermost layer of the cortex. The cells are characterized by the Casparian strip which develops on the anticlinal walls. The Casparian strip is an integral part of the primary wall and is suberized. In citrus roots, the Casparian strip is well differentiated by

the time the primary xylem is mature (65). The deposition of suberin lamellae on cellulose primary walls of the endodermal cells begins a few millimeters to several centimeters behind the tip (38). Suberization occurs initially opposite the phloem poles and gradually extends towards the xylem. At first, one or more cells opposite the xylem poles remain unsuberized, apparently serving as passage cells. Complete suberization is often delayed until after the development of secondary xylem. The suberin lamellae remain relatively thin, and no tertiary thickening occurs in the endodermal cells of citrus roots. Although root type and rate of elongation were not taken into account, Cossmann (38) considered that differences between rootstocks were apparent in the time of occurrence of suberization. The deposition of suberin lamellae occurred early in sour orange, grapefruit and shaddock, and comparatively late in sweet lime, sour lemon, citron, 'Baladi' orange, and rough lemon.

Citrus roots develop a hypodermis, which is a morphologically distinct layer of cells adjacent to the epidermis. The cells of the hypodermis may develop in several ways (65, 118): (a) the outer periclinal and outer regions of the anticlinal walls may become thickened and impregnated with wound gum, and the inner walls suberized; (b) frequently, the cells undergo periclinal divisions, the resulting layer functioning as a phellogen to produce a periderm; (c) groups of cells may enlarge radially and tangentially, rupture the

epidermis, and form hypodermal absorbing areas; or (d) lenticels may form.

Several types of epidermal cells occur: (a) root hairs may form; (b) the outer walls may become thickened and yellow to olive-brown in color; or (c) the outer periclinal walls may remain thin and later collapse or rupture (38, 65, 118). The outer surface of the root is coated with mucigel (17).

In marked contrast to deciduous fruit trees, where the cortex begins to break down after 1 to 4 weeks (5), the cortex in citrus roots is persistent and in roots with little or no secondary growth the cortical tissues remain unchanged throughout the life of the root (118).

#### Root Hairs

Root hairs on citrus roots are typically short and are most abundant near the tip (32, 38, 65). Under the most favorable conditions their length rarely exceeds 0.1 mm. Cossmann (38) found the average length to range from 0.03 to 0.05 mm. The root hairs may occur in patches, horizontal banded areas, or be more or less uniformly distributed with every other epidermal cell developing as a root hair (65). Their shape is variable; tubular, spatulate, papillate, and irregular forms have been observed (32, 38, 59, 65). They are persistent and may remain after the hypodermal periderm is well developed (65). However, it is unlikely that they are functional at this stage as the walls

are thickened and give staining reactions indicating the presence of suberin and possibly lignin. Secondary root hairs may also develop through the elongation of single hypodermal cells as the epidermis breaks down (65).

The length and abundance of root hairs are influenced by environmental conditions. Girton (59) found that the optimum temperature for development was 33°C and that the optimum pH was 5.0. At high pH, root hair development is limited to the formation of primordia (63). Root hair development is reduced by high chloride levels (63) and under conditions of poor aeration (59). Cossmann (38) obtained some evidence that the length, abundance, and location of root hairs would vary with soil moisture conditions, and that the exact response would depend on rootstock. Under field conditions, Castle and Krezdorn (32) found no evidence of an effect of rootstock or of soil depth on root hair characteristics.

#### Non-Growing Roots

An individual root is not necessarily restricted to a single cycle of growth (39). Elongation may cease in response to internal factors or adverse environmental conditions and recommence when conditions again become favorable for growth.

In actively growing roots the root tip is white and succulent with a prominent root cap (118). Non-growing root tips are brown with greatly reduced and flattened root caps. Anatomical changes occurring in the root tip when

elongation ceases have been studied in citrus by Hayward and Blair (63). Cells of the epidermis and hypodermis adjacent to the root cap become deeply stained. There is a progressive extension of this reaction that involves one or more layers of root cap cells lying just outside the apical meristem. These cells become thick-walled and suberized. The cells in the distal portion of the root cap, outside the suberized layer, die. The formation of this suberized layer in the root cap is termed metacutization (136). In dormant apices, only the apical part of the meristem is perpetuated through dormancy. The proximal extremities of the meristem are matured into primary tissues.

The resumption of active growth by a dormant root is initiated in the meristematic cells of the growing point and in pericycle cells adjacent to it. The combined activity of these cells produces a broadened growing point which forms new root cap cells inside the metacutis. As growth proceeds, the old root cap and metacutis are ruptured and displaced laterally. The activation of the pericycle cells forces the endodermis toward the periphery of the root and a separating zone is formed between the cortex of the old and new growth. In citrus roots, a constriction remains visible between the most recent flush and the previous growth flush (118).

#### Secondary Growth

Differentiation of the vascular cambium appears first on the inner edges of the phloem strands, and the early

production of secondary xylem occurs at about the time the late metaxylem elements mature (118). In small citrus roots, cambium formation and the production of secondary xylem is limited to the inner edges of the phloem strands. In larger roots, the cambium differentiates laterally in the pericycle and over the protoxylem poles, forming a complete cylinder.

With expansion of the vascular cylinder, by the production of secondary xylem and phloem, longitudinal cracks occur in the epidermis, hypodermis, and outer cortical cells. Periderms form centripetal to the cracks in the hypodermis and cortex. As expansion increases a periderm forms in the pericycle. Cambial activity in citrus is slow, and the cortex and cortical periderms persist for some time. In roots which undergo substantial secondary thickening, such as pioneer roots, the entire cortex eventually sloughs off.

The seasonal initiation of cambial activity and the extent of secondary thickening shown by individual roots are very irregular (24, 69). In citrus, Cameron and Schroeder (24) observed a relatively slow basipetal progression of cambial activity from twigs to roots. Activity was first evident in twigs and small branches bearing new shoot growth in spring, and was not evident in small roots until the fall. The duration of cambial activity was about 1 month in small roots and 5 months in the major laterals. More detailed observations in deciduous fruit trees (69) have



shown that individual roots may thicken for a period of years and then stop, and not start thickening again for several years. Some roots were observed to persist in the soil as isolated steles for many years.

#### Rates of Growth

The rate of elongation of individual roots of woody plants varies from less than 1 mm/day to more than 25 mm/day during the period of most active growth (82). Only limited data are available for citrus. Crider (39) observed average rates of elongation ranging from 1.3 to 4.3 mm/day, and Waynick and Walker (131) noted that citrus roots grew from 3 to 12 mm/day. These values are similar to values reported for other fruit trees (10, 71, 110). Data for pecan show that root growth rates will depend on root type and order of branching (140). A rate of elongation as high as 25 mm/day was observed for the primary root, whereas the maximum elongation rates for first and second order laterals were 11 and 2 mm/day, respectively. In plum, Bhar et al. (10) found a significant correlation ( $r = 0.52$ ) between elongation rate and root diameter.

Diurnal variation in elongation rates has been observed in several tree species, including citrus (39, 66, 73). Rates of growth were higher at night than during the day. Whether diurnal rhythms are caused by internal periodicity of photosynthesis, translocation, or transpiration has not been determined (73, 87). Analysis of time-lapse

films of growing apple roots showed that the apical 1.5 to 2.0 mm of the root undergoes rhythmic nutational movements as it grows through the soil (66).

Seasonal variations in elongation rates have been observed, and, in general, the highest rates occur in spring or early summer (10, 39, 80).

Rates of secondary thickening have only been reported for apple (69). The largest annual increment recorded was an increase in diameter of 3.7 mm by a root initially 3.2 mm in diameter. The maximum rate of thickening was an increase in diameter of 1.84 mm in a period of 27 days.

#### Formation of Laterals

Lateral branch roots arise endogenously from the pericycle of the parent root (44). In citrus, the earliest laterals are initiated at about the time the metaxylem is maturing (65). If the parent root has more than two xylem poles, the lateral primordia arise opposite these poles. In diarch roots the lateral primordia form to the sides of the xylem poles. As the lateral root develops it ruptures the cortex of the parent root. At first, endodermal cells adjacent to the tip compensate for its growth by undergoing anticlinal divisions, but ultimately the endodermis is stretched and broken. Before the lateral root emerges on the surface of the parent root, the apical meristem, the primary tissue regions, and the rootcap are clearly delimited. Ontogeny and final structure of the lateral root

resembles that of the parent root, but there is wide variation in the number of protoxylem strands.

Factors affecting the initiation and subsequent emergence of lateral roots have been little studied in fruit trees. It is clear, however, that the development of lateral roots is considerably influenced by environmental factors. Increased lateral branching has been observed in soil layers of high nutrient content (87, 114). In pine, increasing the soil temperature from 15 to 25°C resulted in a marked increase in the number and length of laterals (16). Lateral development was almost completely suppressed in the soil at 11°C. Reduced lateral development at low temperatures has been observed in solution culture experiments with citrus (59) and deciduous fruit trees (95).

Lateral root development is inhibited for some distance behind the tip of actively growing roots. In incense cedar, Wilcox (137) found in roots of all orders that the faster the rate of growth, the greater the distance from the root tip to the first lateral root primordium. A similar relationship between root growth rate and distance from the tip to the first lateral root primordium and to the first emerging lateral was also observed in red pine (138). The zone of lateral root development is considered to be regulated by the interaction of a basipetally moving inhibitory substance (possibly cytokinin) from the root tip and acropetally moving promoters originating in the shoot (129, 134, 135).

### Mycorrhizae

Mycorrhizal fungi associated citrus roots are vesicular-arbuscular (VA) mycorrhizae (58). These fungi are a type of endomycorrhiza, and form complex coils and loops within the cortical cells and a loose network of hyphae in the soil. Citrus is apparently highly dependent on the mycorrhizal association. Stunting and nutrient deficiency symptoms in fumigated soils have been associated with a lack of mycorrhizal infection (81).

The main benefit of the mycorrhizal association is enhanced nutrient uptake, in particular, phosphate and zinc (58, 90). Gerdemann (57) suggested that woody plant species that lack or have relatively poorly developed root hairs were likely to be more dependent on VA mycorrhizae. Unlike ectomycorrhizal fungi, VA mycorrhizae produce very little change in root morphology, and there is no evidence that the extent of lateral branching or root longevity is affected (57).

### Longevity

Root shedding is considered to be a natural part of the development of healthy perennial plants (71). Only a small proportion of the roots produced by a tree survive for many years. The greatest natural loss from tree root systems occurs among the fine fibrous roots, and much of the annual loss of fine roots apparently occurs during the winter months (71, 82). Large numbers of partially decayed

fibrous roots have been observed in citrus during winter and early spring (124).

The length of time citrus fibrous roots persist or remain functional is not known. In apple, fine roots have been observed to decay after only 2 to 3 months, whereas in other species fine roots have remained alive for at least 3 years (71). In citrus, the loss of fibrous roots has been intensified by severe pruning (13) and freeze injury (51). Severe root losses can occur as a result of unfavorable soil conditions and disease (71).

#### Water and Nutrient Uptake in Relation to Development

The concept of a limited absorption zone confined to the unsuberized apical region of the root is no longer tenable (5, 35, 36, 84, 94). Although higher rates of uptake have been observed for unsuberized regions, evidence is available for several woody perennials (7, 8, 16, 35, 83, 84), including citrus (34, 40, 64), that suberized and secondary thickened roots can also function in water and nutrient uptake. At certain times of the year, during winter and in drought periods, when active root growth is suppressed, uptake must occur exclusively through suberized roots (84).

The term suberization is used to describe three different aspects of root development (94): (a) the deposition of suberin lamellae on the inside of the cell walls of the endodermis; (b) the deposition of suberin in the cell walls

of the hypodermis; and (c) periderm formation as a consequence of secondary growth. Passage across the suberized endodermis is provided by large numbers of plasmadesmata (37). Access through the periderm of older roots is thought to occur through lenticels, breaks around branch roots, wounds, and between the discontinuous platelets of periderm that occur in some species (1, 35). The functional significance of the hypodermis in citrus has not been studied. The development of a suberized hypodermis in maize roots severely restricted the translocation of phosphate and calcium, and was a more important barrier than the endodermis (46). In citrus, the occurrence of hypodermal absorbing areas may be of considerable importance (65).

Although considerable changes in structure occur as the root ages, these developmental changes do not entirely prevent water and nutrient uptake by older roots. However, it is likely that there will be increasing discrimination against nutrients that cross the cortex in the apoplast (36). Thus, the uptake and translocation of calcium is largely confined to the unsuberized apical region of the root (61). The apices of elongating roots, by continually exploring the soil, may also be the main source of supply for nutrients which diffuse slowly in the soil (36).

## Seasonal Periodicity of Root Growth

### Basic Pattern

Root growth in tree crops follows an irregular time course. The pattern varies with species and is greatly affected by environmental factors, in particular, soil temperature and soil water stress (87). There is still uncertainty about the extent to which the observed patterns of growth are caused by internal factors or are induced by environmental conditions (29, 71, 87).

The two basic components of the growth of tree root systems are (a) extension growth, and (b) radial thickening to form the woody framework. Few studies have considered radial growth or the relationship between radial growth and extension growth (45). Most studies of the seasonal periodicity of root growth have been concerned with extension growth, which involves the continued elongation of existing roots and the initiation and subsequent elongation of new laterals. Usually no attempt has been made to distinguish between these two components of extension growth or to differentiate between the growth behavior of different types of roots, although these aspects may be important to a complete understanding of the seasonal periodicity of root growth (82, 101).

The growth periodicity of citrus roots was first studied by Crider (39) in Arizona, who grew seedling and young budded trees in large glass-faced containers. Crider

observed that citrus roots did not grow continuously throughout the year but showed distinct growth and rest periods of rather definite duration. Root growth commenced in late March or early April, underwent three cycles of active growth, and ceased in late October or early November. Although the root system as a whole underwent three cycles of active growth throughout the year, the number of cycles shown by individual roots ranged from 1 to 3. An individual root did not necessarily elongate for the entire period of a particular cycle and in some cases growth lasted only a few days. Total growth and the rate of elongation were greatest during the spring growth cycle and least during the summer growth cycle.

Three cycles of active root growth throughout the year have also been observed in citrus in California (131) and Florida (62). In these studies plate glass observation panels were installed against vertical profile walls under the edge of the canopy of established field trees. The trees in California were on sour orange rootstock and root growth was evident during the following periods: late March to early April, late May to mid-June, and early September to early October. In spring, root growth in the subsoil preceded growth in the top 30 cm by 28 days. The trees used in Florida were on sour orange and trifoliate orange rootstocks. Similar to observations in California and Arizona, the resumption of growth in spring occurred in late March or early April. The time of occurrence of the second



and third growth cycles, however, varied greatly between individual trees. In the fall, root growth ceased as early as September in some trees, whereas in other trees root growth continued through November and December. No consistent differences between rootstocks were evident in the pattern of growth.

Under different climatic conditions different patterns of root growth have been observed. In South Africa, Marloth (88) studied the periodicity of citrus root growth by excavating young trees on rough lemon and sweet orange rootstocks from nursery rows at weekly intervals. The intensity of root growth was recorded on an arbitrary scale, based on the abundance of newly-formed white root tips. Two major periods and three minor periods of root growth activity were observed during the year. Reflecting the mild winter conditions of the region, the longest and most active period of root growth occurred during winter. The second major period occurred during summer. Rough lemon showed some degree of activity throughout the entire year, while sweet orange showed periods of dormancy.

Active root growth during part or throughout the entire winter season has also been recorded in Israel, in established field trees on sweet lime and sour orange rootstocks (38, 93). Root growth activity was assessed by estimating the abundance of white root tips in samples collected at a depth of 30 cm. No clear indication of the annual number of growth cycles was obtained, as fluctuations in the

intensity of root growth during summer were governed by the timing of irrigations (93).

#### Effect of Soil Temperature

In temperate regions, the reduction or complete cessation in root growth activity during winter is due to low soil temperature (87). The minimum temperature at which citrus roots will elongate is approximately 12°C (59, 96). Under field conditions, no root growth has been observed where soil temperatures were below 13 to 14°C (93, 131). In South Africa (88) and Israel (38), where root growth has been observed throughout the winter period, the lowest mean minimum soil temperatures recorded were above 14°C.

In regions where soil temperatures are limiting for root growth during winter the resumption of growth in the spring is delayed until soil temperatures exceed the minimum for growth. Thus, in California, Waynick and Walker (131) reported that the average subsoil temperature at the time root growth resumed in late March was 13.8°C. With increasing soil temperature during early spring, Cossmann (38) observed a rapid increase in the intensity of root growth. During summer, Monselise (93) found that very intense root growth was often associated with soil temperatures of 29°C and above, provided soil moisture was not limiting. In controlled experiments, maximum citrus root growth is generally observed between 26 and 32°C (27, 59, 96, 97).

In general, the effect of soil temperature on root growth predominates during fall, winter, and early spring. The response to increasing soil temperature during spring and summer is often confounded with increasing soil water deficits and the occurrence of shoot growth. Thus, Marloth (88) found no specific correlation between soil temperatures above 14°C and the periodicity of citrus root growth. Significant correlations ( $r = 0.73$  and  $r = 0.48$ ) between the overall pattern of root growth activity and variations in mean soil temperature have been only reported for raspberry (3).

#### Effect of Soil Water Stress

When soil temperatures are non-limiting, the main edaphic factor affecting root growth is soil water availability. Decreased root growth activity as a result of low soil water availability has been observed in citrus (93) and other tree crops (41, 76, 106, 110, 128). The reduction in root growth activity is especially pronounced during periods of high evaporative demand in summer.

There is very little experimental evidence on the level of soil water stress at which root growth first becomes affected. In early studies no attempt was made to distinguish between the effects of water stress on the continued elongation of existing roots or on the emergence of new laterals. Recent work has shown that these two components of growth respond differently to a given level of

stress (85, 128). Monselise (93) found that citrus root growth was very limited at soil water tensions of 7.5 to 8 bar. In sand, no root growth was evident at higher tensions. In other tree species, reduced root growth activity has been detected at much lower tensions. Rogers (110) reported that apple root growth was checked at a tension of 0.4 to 0.5 bar, and with Sitka spruce growing in a peat soil, Deans (41) found that the minimum soil water tension at which root losses first occurred was less than 0.2 bar. In white oak, Teskey and Hinckley (128) found that the maximum rate of root elongation occurred at a soil water potential of -0.5 bar and decreased linearly with decreasing soil water potential. In contrast, the maximum number of growing roots occurred at -5.0 bar. Enhanced root production with decreasing soil water availability was interpreted as a drought resistance mechanism. Reduced extension growth with decreasing soil water potential (from -1 to -6 bar) has also been reported for white and loblolly pines (77).

Water potentials developed around plant roots are largely determined by plant demand and hydraulic conductivity. Thus, the response to a given level of stress may vary for different soil types and at different times of the year. The effect of plant demand was noted by Kaufman (76). Low levels of available water concurrent with periods of high evaporation were accompanied by marked reductions in root growth activity. At moderate rates of evaporation

the effect of low soil water availability was less pronounced. Under conditions of low atmospheric stress, Werenfels (133) reported that apple roots extended into regions with soil water tensions of 0.7 to 7.7 bar equally fast, provided the mean soil water content was high. Lyr and Hoffmann (87) have emphasized that the response to localized soil water deficits may depend on conditions experienced by other parts of the root system.

#### Relationship to Shoot Growth

Shoot growth in citrus occurs in a series of flushes. In temperate and sub-tropical zones there are usually 3 to 4 flushes a year in bearing trees, with the major flushes occurring in spring and early summer. In most studies the first cycle of root growth has followed the spring shoot flush (39, 62, 93, 102, 117). There is only one report of root growth preceding shoot growth (131). In Marloth's (88) study with young trees in South Africa, where root growth was more or less continuous throughout the year, no such distinction was possible. In citrus, it is apparent that the initiation of shoot growth in spring is not dependent on active root growth; a point also confirmed under controlled conditions (141). With evergreen trees it is generally considered that root growth is either continuous or is resumed independently of shoot growth when the soil temperature is high enough (87, 141). In deciduous trees there is some evidence that the initiation of new root

growth in spring requires a stimulus, apparently auxin, from a physiologically non-dormant shoot system (87, 107). Root growth is generally evident before bud expansion because of a lower temperature optimum for growth.

During spring and summer a general trend towards alternation of root and shoot growth has been observed (39, 62, 88, 93, 102, 117, 131). However, there is some divergence of opinion as to its significance. Thus, Marloth (88) considered that variations from the general trend were sufficiently frequent and large to cast doubt on alternation as a basic physiological characteristic of citrus. Schneider (117) observed that root growth overlapped the second and third flushes of shoot growth. In other studies, although definite alternation was evident in spring and early summer, concurrent root and shoot growth occurred during late growth flushes (93, 131). These inconsistencies may be accounted for by differences in plant material or in the environmental conditions under which the various studies were conducted. However, a major difficulty in interpreting the above results is that in none of the studies was the intensity of both root and shoot growth measured in an objective manner. Either the time of occurrence of shoot growth was simply recorded or its intensity estimated on an arbitrary scale. More detailed studies carried out with deciduous fruit trees have shown that reductions in the intensity of root growth during the period of shoot growth depended on the intensity of shoot growth (67, 68). Branch

pruning stimulated more intense shoot growth, and the more intense the shoot growth the greater and more prolonged the reduction in new root growth. There was some evidence that the amount of root growth occurring after the cessation of shoot growth was positively related to the intensity of shoot growth which preceded it. Alternation of root and shoot growth in fruit trees has been attributed to competition between roots and shoots for assimilates (5) or to inhibition of root growth by high levels of auxin produced during active shoot growth (93, 139). This interrelationship between root and shoot growth appears to be the major factor affecting the intensity of root growth in citrus at times when soil temperatures are non-limiting and the soil water supply adequate.

In bearing fruit trees the pattern of root growth is also greatly affected by crop load (70, 110). Atkinson (5) concluded that cropping was likely to be responsible for much of the year-to-year variation in root growth. The effects of cropping on root growth have not been studied in citrus.

#### Root Observation Techniques

The technique of installing glass panels adjacent to the soil profile has been used for many years to study the life history and growth dynamics of tree root systems (5, 14). The principle advantages of the method, according to

Atkinson (5), are (a) a series of direct and detailed measurements can be made on the same roots or on the same part of the root system over a long period of time, without disturbing the roots; (b) special photographic methods such as time-lapse cinematography can be used; and (c) the relationship of root growth to environmental variables can be readily studied. The method has been used successfully with several tree species (8, 10, 67, 68, 80, 87, 89, 110, 128), including citrus (39, 62, 131).

Field studies have been carried out by installing observation windows against vertical profile walls in trenches excavated near established trees (62, 80, 110, 128, 131), or by planting young trees adjacent to the windows of permanent underground laboratories or rhizotrons (8, 10, 67, 68, 87, 89). The observation windows are covered with shutters to exclude light. A problem with installations against established trees is that several large diameter roots usually have to be pruned which may stimulate abnormal patterns of root growth during the first year (80, 110). Planting young trees adjacent to permanent observation laboratories overcomes the problem of severe pruning. Observation laboratories consist of an underground walkway with windows on either side. They have been constructed with the windows adjacent to an undisturbed natural profile (113) or with compartments that are filled with soil (72). Temperature fluctuations at the windows are normally very similar to temperatures measured in the bulk soil (14).



Root growth of young trees has also been studied by using glass-faced containers (39, 111, 138). Crider (39) used containers 0.9 and 1.8 m in depth to study citrus root growth, and Wilcox (138) used containers 0.6 and 1.5 m in depth in his studies with red pine. The use of containers allows individual environmental factors to be isolated. In a few studies the containers have been installed below ground at field sites (14). This exposes the shoots to a normal field environment and the roots experience natural soil temperatures. The containers are periodically raised above ground to record root growth. Bohm (14) concluded that the larger the rooting volume of the container, especially in the vertical direction, the more satisfactory the results.

Exposure to light during recording is unavoidable. The effect of light on apple root growth was studied by Rogers (111). Although continuous exposure to light severely checked root growth, hastened suberization and reduced the development of lateral roots, exposure for brief periods of time had considerably less effect. The reduction in root length caused by weekly exposure for 30 minutes was only significant in summer, when light intensity was high, and was not significant in late summer or fall. It was concluded that exposure for short periods of time for recording was unlikely to have any serious effects on the results. Pearson (100) studied the light sensitivity of a number of species and found no difference in elongation

rate due to light exposure with corn, tomato, cotton, and soybean. In contrast, light appreciably reduced the growth rate of peanut roots, and it was suggested that the light sensitivity of each species to be studied should be checked. No information is available for citrus.

Two types of material have been used for the observation windows. Early studies were conducted with plate glass. In more recent times acrylic plastic (Plexiglas) has also been used. Acrylic plastic windows have been used in observation laboratories (123, 125, 126), observation trenches (47), and in container studies (119) with various crops. There is limited evidence (130) that elongation rates along a soil-plastic interface may be less than rates in bulk soil, which was attributed to the charge nature of the surface of the plastic. Taylor and Bohm (126) observed that adhesion between soil and glass windows was greater than between soil and plastic windows, and subsequently found in a study with soybeans that rooting density at the soil-plastic interface was substantially greater than in the bulk soil. However, there were no visual differences between roots at the interface and roots from the bulk soil. They concluded that acrylic plastic windows would be satisfactory for phenological studies, but that glass windows should be used for studies involving rooting density.

## MATERIALS AND METHODS

### Seasonal Pattern of Root Growth Study

This study was conducted at the Agricultural Research and Education Center, Lake Alfred, in central Florida over a period of 16 months from August 1981 to November 1982.

#### Trees

Sixteen-month-old 'Valencia' orange (Citrus sinensis (L) Osb.) trees on rough lemon (C. jambhiri Lush.) and Carrizo citrange (Poncirus trifoliata (L) Raf. X C. sinensis) rootstocks were obtained from a commercial nursery and were planted singly in root observation chambers on August 4, 1981. There were 3 trees on each rootstock. The trees were lifted bare-root from the field nursery according to usual commercial practice. No additional pruning of the root system was carried out prior to planting.

Except during the period when water stress treatments were imposed, all trees were kept well-watered. The trees were fertilized with a complete nutrient solution 1 or more times a month, depending on growth activity, and were sprayed for pest and disease control as required.

### Root Observation Chambers

Six chambers were constructed. Each chamber consisted of a 88 x 15 x 180 cm high planting compartment which drained into a lower compartment (Figure 1). The basic frame was constructed from 5 x 20 cm pressure-treated timber. The sides of the chambers were constructed from 6.4 mm transparent Plexiglas sheets which provided two 88 x 180 cm observation panels and a total viewing surface of  $3.17 \text{ m}^2$  for each chamber. The Plexiglas sheets were sealed to the timber frame with silicone caulking and fastened with screws through strips of flat iron. Channel iron bars placed horizontally across the chamber and attached to the timber frame were used to reinforce the Plexiglas sheets at 45 cm intervals (Figure 1). The reinforcing bars on opposite sides of the chamber were connected with a bolt inserted through the chamber. The reinforcing bars divided each observation panel into 4 windows of approximately equal area. Each window was covered with a galvanized sheet metal shutter to exclude light. The shutters were attached to the timber frame with screws. Drainage from the planting compartment occurred through a single mesh-covered outlet in the base of the compartment. Each chamber was seated in a metal frame which supported the chambers during lifting.

### Soil

For this study each chamber was filled with untreated Candler fine sand obtained from an orchard site. The soil

Figure 1. Side views of a root observation chamber.  
A) Entire chamber raised above ground with chain hoist, metal shutters cover the observation windows of the planting compartment; B) close-up of Plexiglas observation windows.



was collected in layers so that the natural soil profile could be reconstituted in the chambers. Each chamber was filled by carefully adding soil in 5 cm layers. After each layer was added, the soil was lightly tamped to ensure uniform packing throughout the full depth of the chamber.

Certain physical and chemical characteristics of the chamber soil environment were determined on samples collected from chambers which were dismantled in September, 1982. Soluble salts, pH, Ca, Cu, K, Mg, and P were determined on samples collected from the 0-15, 15-45, 45-90, 90-135, and 135-180 cm depth zones. Calcium, Cu, and Mg were determined by atomic absorption spectroscopy, K by flame emission spectroscopy, and P colorimetrically, following double-acid extraction. Core samples were taken from each depth zone for determination of the soil moisture characteristic using Tempe pressure cells (103) and bulk density.

#### Field Installation

The chambers were retained above ground for the first 4 months of the study, as construction of the permanent field site had not been completed. The chambers were located in partial shade and were exposed to ambient air temperature. On December 9 the chambers were installed below ground. The permanent field site consisted of 3 separate underground retaining frames constructed from angle iron and sheet metal (Figure 2). The frames were arranged in a



Figure 2. General view of field site showing chambers installed in underground frames and track for chain hoist. Instrument for recording soil temperature is housed in the shelter.



single row oriented in a north-south direction. Each frame accommodated 2 chambers. One tree on each rootstock was assigned at random to each location. Throughout this report the rough lemon and Carrizo citrange tree assigned to location 1 will be referred to as RL-1 and CAR-1, respectively, and similarly for locations 2 and 3. To record root growth the chambers were raised above ground by means of a manually operated chain hoist (Figure 1). The hoist was centered above each chamber by moving the lifting frame along a track parallel with the chambers (Figure 2). During January, plastic shelters were used to protect the trees from cold damage.

Soil temperatures were measured with thermocouples installed adjacent to an observation panel at depths of 15, 30, 45, 60, 90, 120, and 150 cm in 1 chamber. Thermocouples were also installed at a field site to provide a comparison between chamber and natural soil temperatures. Data were recorded automatically every hour on a strip recording chart. Tensiometers were installed in 4 chambers at depths of 22, 67, 112, and 150 cm to monitor changes in soil water tension and to schedule irrigation requirements.

#### Growth Measurements

During 1981 root growth was recorded at weekly intervals in all chambers. During 1982 root growth was recorded at 1 to 2 week intervals in RL-1 and CAR-1, and at 1 to 4 week intervals in the remaining chambers. On each observation date, the amount and position of new root growth was

recorded by using transparent acetate overlays to trace the root system. Different colors were used to distinguish particular observation intervals. A separate series of sheets was maintained for each of the 8 windows of each chamber. During recording, only 1 window was exposed at a time and care was taken to avoid exposure to direct sunlight. The time required for each observation ranged from 5 to 20 minutes per window, depending on the amount of new root growth.

During shoot growth flushes the total increase in length of all growing shoots was recorded at approximately weekly intervals.

#### Water Stress Treatments

To obtain information of the effect of soil water stress on the pattern of root growth, water was withheld from trees RL-1 and CAR-1 for an initial period of 14 days, and after rewatering, for a second period of 8 days during August 1982. RL-2 and CAR-2 were maintained as well-watered controls and in these chambers the mean soil water tension did not exceed 0.2 bar. Root growth was recorded at 2 to 4 day intervals. Xylem pressure potential was measured with a pressure bomb on 3 exposed leaves per plant. Measurements were made between 1300 and 1400 hours DST.

## Morphological Development of the Root System

### Nursery Trees

At the time the chambers were planted, an additional 10 trees on each rootstock were obtained from the nursery and the length, volume, surface area, and dry weight of the taproots, main laterals, and fibrous roots were determined. Total length of fibrous roots was estimated from their dry weight. The relationship between length and dry weight was determined separately for each rootstock by measuring the length of four 5 m subsamples on mm graph paper. The length of taproots and main laterals was measured directly. Root volume was determined by displacement of water. Surface area was calculated from the length and volume determinations (6).

### Chamber Trees

The entire root system of RL-2 and CAR-2 was recovered from the chambers in September 1982, 13 months after planting. The root system was recovered by removing one of the observation panels and inserting a needle board with needles spaced at 5 cm intervals (14). The observation panel on the opposite side of the chamber was then removed and the root system exposed by gently washing away the soil. By using the needle board the natural spatial distribution of the root system was retained. The origin of roots comprising the root system framework was recorded and the length, volume, surface area, and dry weight of all

components of the root system were determined in the manner described for the nursery trees. Additional subsamples were used to determine the relationship between length and dry weight for fibrous roots.

#### Exposure to Light Study

For this study 6-month-old Carrizo citrange seedlings were planted in 27 x 5 x 88 cm high root observation boxes containing Candler fine sand in August 1982. Treatments consisted of 3 light exposure regimes and 2 types of observation panel. The light treatments were (a) observation panel uncovered at all times; (b) observation panel exposed to light for 1 hour per week; and (c) observation panel not exposed. The 2 types of material used for the observation panel were glass and Plexiglas. The light treatments were initiated on September 2 and continued for 8 weeks. Each of the 6 treatment combinations was replicated twice. The boxes were arranged in randomized blocks in an open-sided greenhouse.

In treatments where the observation panel was exposed, new root growth was recorded at weekly intervals by tracing on transparent acetate sheets. From these records root elongation rates were determined. At the end of the experiment, the total increase in length and number of main roots and lateral roots was determined for all treatments. The data were analyzed as a 3 x 2 factorial by analysis of variance.

## RESULTS AND DISCUSSION

### Soil Characteristics

The soil used in the chambers was a reconstituted profile of Candler fine sand and showed no marked changes in texture to a depth of 180 cm. The water retention capacity of the soil was low (Figure 3). At a pressure potential of -0.1 bar the mean soil water content was 4.8% by volume. At the wilting point (pressure potential of -15 bar) the mean soil water content was 0.7% by volume. Soil bulk density ranged from 1.48 to 1.57 g/cm<sup>3</sup> (Table 1).

Mineral nutrient concentrations were highest in the surface horizon and generally declined sharply with depth (Table 2). The values are typical of deep sandy soils in central Florida (28). Soil pH decreased from 6.3 at the surface to 5.8 at 135 to 180 cm (Table 2).

Characteristics of the soil in the chambers were generally similar to the characteristics of comparable field soils (28). There were no indications of soil conditions detrimental to root growth.

Figure 3. Soil moisture characteristic determined on core samples from root observation chambers.

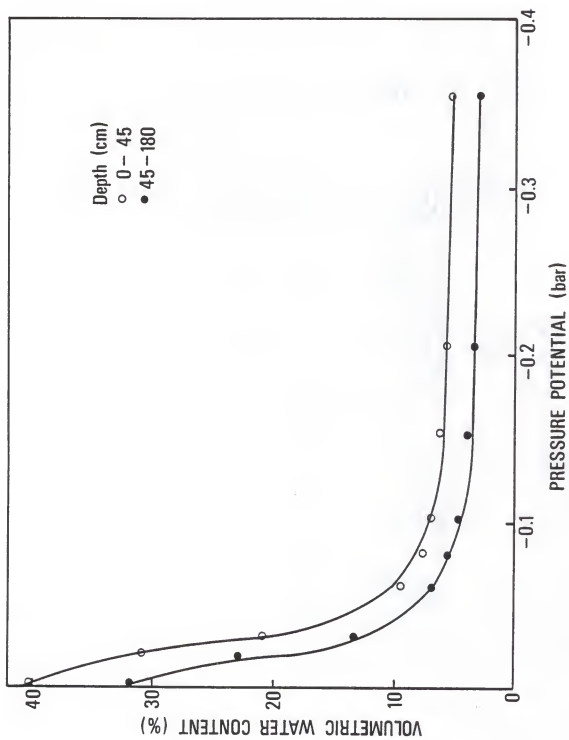


Table 1. Soil bulk density in root observation chambers.

Depth zone (cm)	Bulk density (g/cm <sup>3</sup> )
0-45	1.48
45-90	1.52
90-135	1.51
135-180	1.57



Table 2. Soil pH, soluble salts and mineral nutrient content in root observation chambers.

Depth zone (cm)	pH	Soluble salts (ppm)	Mineral nutrients (ppm)				
			P	K	Ca	Mg	Cu
0-15	6.3	50	50	8	480	20	22.8
15-45	5.9	34	39	4	84	4	1.8
45-90	5.9	34	48	4	136	8	0.8
90-135	6.1	50	25	8	100	4	0.6
135-180	5.8	50	27	8	80	4	0.6

## Seasonal Pattern of Root and Shoot Growth

### Pattern of Growth During 1981

Mean monthly air temperatures between August and December, 1981, are shown in Table 3. At the time of planting, temperatures were near optimum for growth. Temperatures decreased gradually during September and October, but declined sharply during November. As the chambers were retained above ground during this phase of the study, soil temperature was found to be generally similar to ambient air temperature.

Root and shoot growth patterns are shown in Figures 4 to 9. As the growth patterns of different trees were asynchronous, the data are presented separately for each tree. New root growth was observed in all trees prior to the initiation of the first shoot growth flush. New growth was evident 1 week after planting in RL-3 (Figure 6) and was evident at the observation windows of all chambers within 2 to 3 weeks after planting. The rapid appearance of growing roots at the observation windows indicates that, during summer, there is little delay in the resumption of root growth following transplanting.

Prior to the initiation of shoot growth, 3 to 5 weeks after planting, there was a rapid increase in root growth activity at the observation windows. With the onset of the shoot growth flush, root growth declined and remained at a relatively low level until shoot elongation ended.

Table 3. Mean monthly minimum and maximum air temperatures from August to December, 1981 at the Agricultural Research and Education Center, Lake Alfred.

Month	Temperature (°C)	
	Minimum	Maximum
August	22.3	33.2
September	19.4	32.7
October	16.9	31.0
November	9.5	25.7
December	7.5	22.4

Figure 4. Seasonal changes in root and shoot growth activity in RL-1 from August to December, 1981. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.

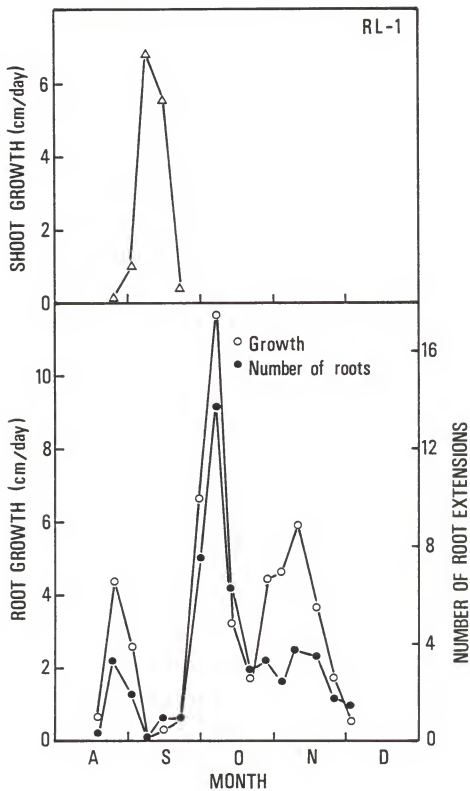


Figure 5. Seasonal changes in root and shoot growth activity in RL-2 from August to December, 1981. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.

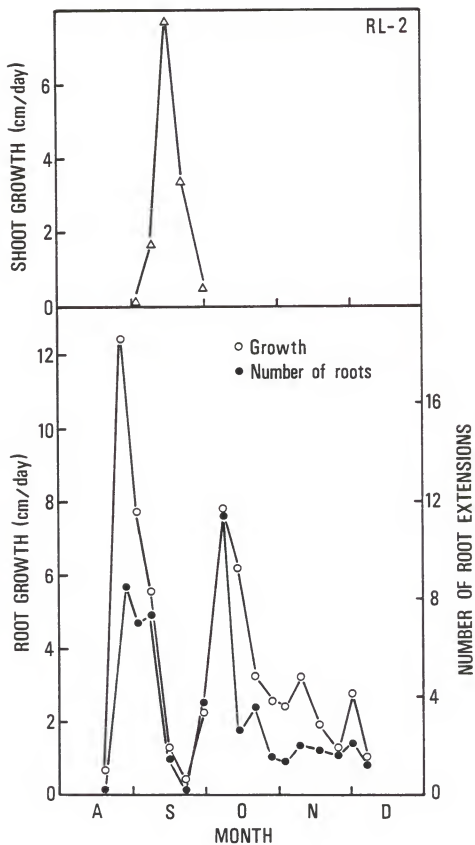


Figure 6. Seasonal changes in root and shoot growth activity in RL-3 from August to December, 1981. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.



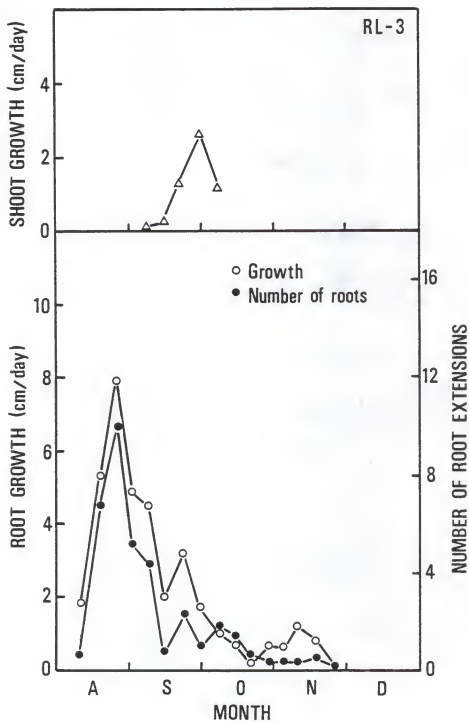


Figure 7. Seasonal changes in root and shoot growth activity in CAR-1 from August to December, 1981. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.

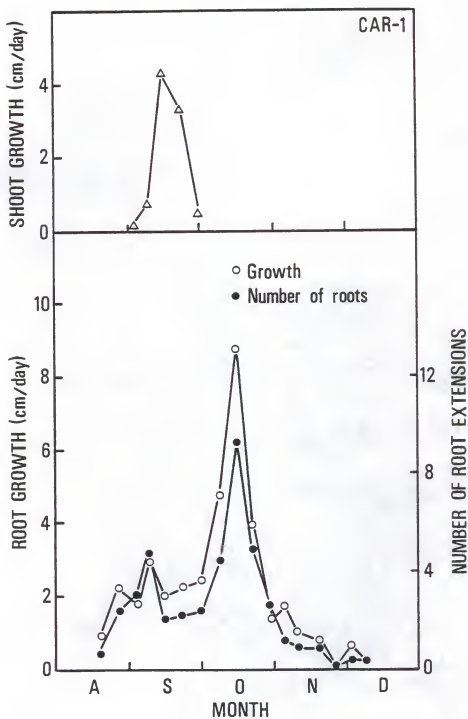


Figure 8. Seasonal changes in root and shoot growth activity in CAR-2 from August to December, 1981. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.

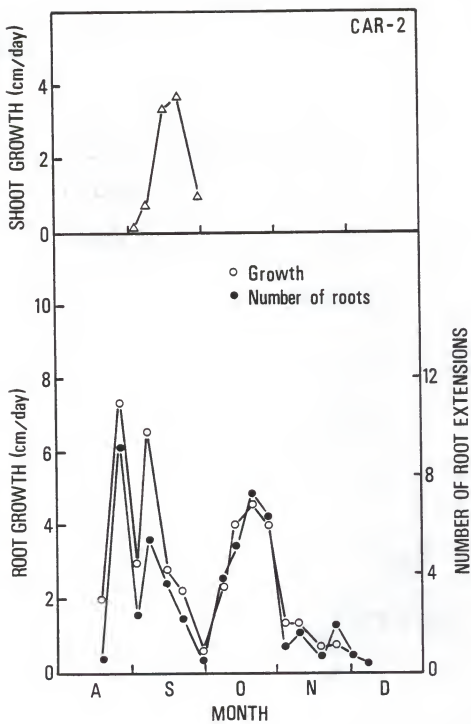
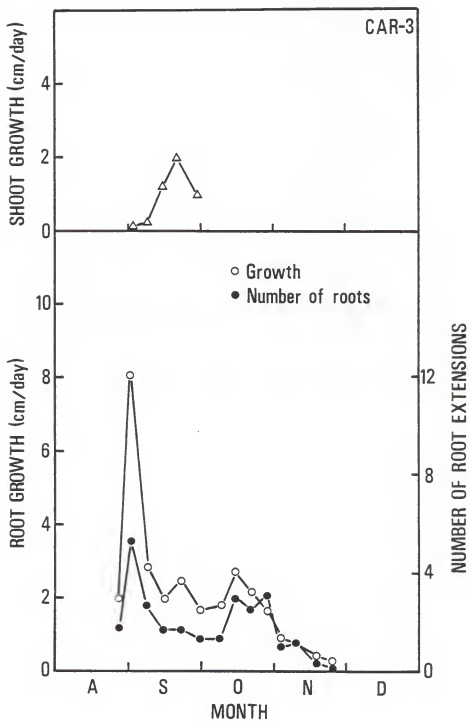


Figure 9. Seasonal changes in root and shoot growth activity in CAR-3 from August to December, 1981. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.



The complete cessation of root growth was observed only in RL-1 (Figure 4). Immediately following the cessation of shoot elongation a marked increase in root growth activity was observed in RL-1, RL-2, CAR-1, and CAR-2 (Figures 4, 5, 7, and 8). Activity increased for a period of 2 to 3 weeks and then declined. No increase in root growth activity was observed in RL-3 (Figure 6) and only a slight increase occurred in CAR-3 (Figure 9). Root growth declined in all trees after mid-October and eventually ceased in late November or early December in response to low temperature (Table 3).

In all trees, the amount of root extension growth that occurred during each observation interval was closely related to the number of roots that grew during each interval (Figures 4 to 9). A similar relationship was observed by Rogers (110) in a study of apple root growth with root observation trenches. There were no significant differences between rootstocks in the total length and number of new roots visible at the observation windows or in the total length and number of new shoots (Table 4).

To examine the seasonal pattern of growth of different types of roots, visible root growth was assigned to 2 basic categories: main roots and lateral roots. Most of the roots classified as main roots were typical pioneer roots (118) and underwent considerable extension growth. The longest visible main root attained a length of 58.8 cm during 1981. Lateral roots were first order laterals



Table 4. Total length and number of roots visible at the observation windows and total length and number of shoots which grew during the period August to December, 1981.

Root-stock	Tree no.	Root length (cm)	No. of roots	Shoot length (cm)	No. of shoots
RL	1	388.4	322	84.7	3
	2	427.9	304	86.3	5
	3	255.9	198	42.2	1
	Mean <sup>z</sup>	357.4	274.7	71.1	3.0
CAR	1	252.4	183	58.7	3
	2	292.2	251	58.7	3
	3	209.1	135	29.9	1
	Mean	251.2	189.7	49.1	2.3

<sup>z</sup>Differences between rootstocks were not significant.

arising from the main roots and underwent limited extension growth. The longest visible lateral root attained a length of 7.2 cm.

The pattern of growth of main and lateral roots is shown in Figures 10 to 13. It is apparent that the major fluctuations in visible root growth activity were largely the result of changes in the pattern of development of lateral roots. Thus, the rapid increase in root growth activity observed after the cessation of shoot growth was due to the development of large numbers of lateral roots.

The emergence of lateral roots occurred only while the main axis was elongating. There was no continued development of laterals towards the tip after growth of the main axis ceased, as has been reported for other species (137). Following shoot growth, several main roots commenced a second cycle of elongation after a period of rest ranging from 11 to 53 days. With the resumption of growth of the main axis the development of lateral roots resumed, both in the normal acropetal sequence and from regions of the root where laterals had developed during the previous growth cycle. The emergence of laterals along older regions of the root was restricted to a short period of time immediately after the resumption of growth of the main axis.

#### Pattern of Growth During 1982

Mean monthly air temperatures during 1982 are shown in Table 5. Mean minimum temperatures ranged from 7.1°C in

Figure 10. Seasonal changes in the number of main roots and lateral roots undergoing extension growth in RL-1, RL-2, and RL-3 from August to December, 1981. Data are expressed as the total number of visible roots which grew between 2 observation dates divided by the number of days in the observation interval. Horizontal bars indicate period of shoot growth.

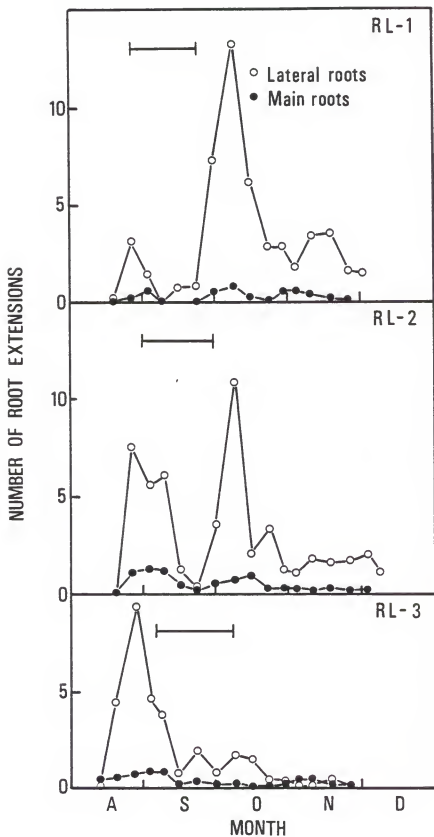


Figure 11. Seasonal changes in extension growth of main roots and lateral roots in RL-1, RL-2, and RL-3 from August to December, 1981. Data are expressed as the total increase in length of all visible roots between 2 observation dates divided by the number of days in the observation interval. Horizontal bars indicate period of shoot growth.

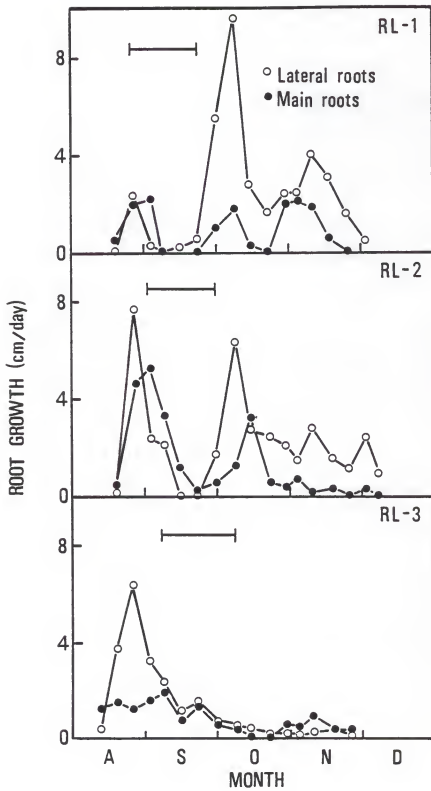


Figure 12. Seasonal changes in the number of main roots and lateral roots undergoing extension growth in CAR-1, CAR-2, and CAR-3 from August to December, 1981. Data are expressed as the total number of visible roots which grew between 2 observation dates divided by the number of days in the observation interval. Horizontal bars indicate period of shoot growth.

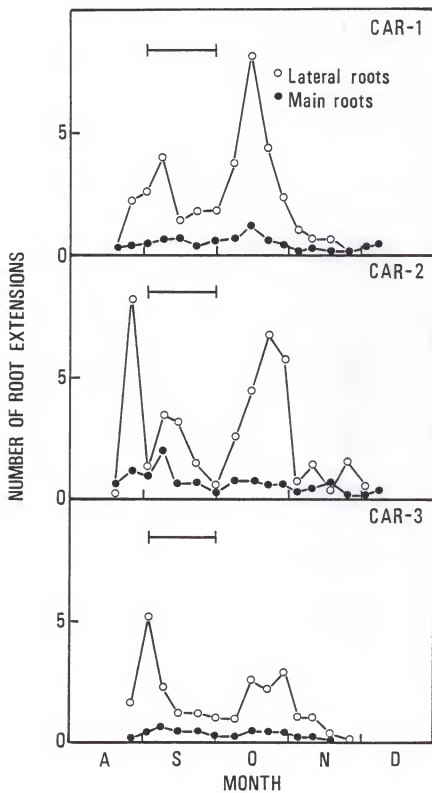




Figure 13. Seasonal changes in extension growth of main roots and lateral roots in CAR-1, CAR-2, and CAR-3 from August to December, 1981. Data are expressed as the total increase in length of all visible roots between 2 observation dates divided by the number of days in the observation interval. Horizontal bars indicate period of shoot growth.



Table 5. Mean monthly minimum and maximum air temperatures during 1982 at the Agricultural Research and Education Center, Lake Alfred.

Month	Temperature (°C)	
	Minimum	Maximum
January	7.1	23.4
February	13.0	26.8
March	13.4	27.7
April	16.1	28.9
May	16.0	30.3
June	22.0	32.6
July	22.2	34.0
August	22.2	33.4
September	21.0	32.3
October	17.2	28.9
November	15.6	27.2
December	12.4	25.5

January to 22.2°C in July and August. Mean maximum temperatures were greater than 23°C in all months and increased to 34.0°C in summer.

Mean soil temperatures, at a depth of 15 cm in the observation chambers, increased from 20.0°C in February to a maximum of 29.4°C in July (Table 6). Differences in mean temperature between 15 and 150 cm in the chambers were slight and were generally less than 2°C. Diurnal variations in temperature were of the order of 8°C at 15 cm and less than 2°C at depths below 45 cm. Soil temperatures in the chambers, in relation to season and soil depth, were similar to temperatures recorded at the field site (Table 6). Soil temperatures observed at the experimental site during 1982 were similar to the 5-year average values reported by DuCharme (42) for Lake Alfred.

Seasonal patterns of root and shoot growth during 1982 are shown in Figures 14 to 19. All trees initiated a shoot growth flush in early January. Shoot elongation continued through January and ceased in early February. As the trees were adequately protected, the developing shoots were not damaged by the freezing temperatures that occurred in mid-January. The main period of shoot growth commenced in April, and between April and October each tree underwent an additional 3 or 4 growth flushes. The timing of the various growth flushes between trees and the intensity of growth during each flush were highly variable. The interval between growth flushes ranged from less than 1 week to as long

Table 6. Mean monthly soil temperatures in root observation chambers and at an adjacent field site during 1982.

Month	Chamber temperature (°C)				Field site temperature (°C)			
	15	45	90	150	15	45	90	150
February	20.0	19.5	18.8	-				
March	23.1	21.7	20.7	-				
April	23.6	23.3	22.5	21.9				
May	24.7	24.1	23.3	22.7				
June	28.3	27.2	26.1	25.5	25.2	24.7	24.0	23.5
July	29.4	28.9	28.3	27.8	28.3	27.8	27.2	26.1
August	29.1	28.7	28.3	27.7	30.0	29.4	28.7	28.3
September	27.3	26.8	26.7	26.2	29.1	28.9	28.6	28.2
October	24.0	24.3	24.5	24.5	28.0	27.4	27.2	27.3
November	21.6	21.6	21.9	22.0	24.0	24.6	25.2	25.7
					21.1	21.7	22.4	23.0

Figure 14. Seasonal changes in root and shoot growth activity in RL-1 during 1982. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.

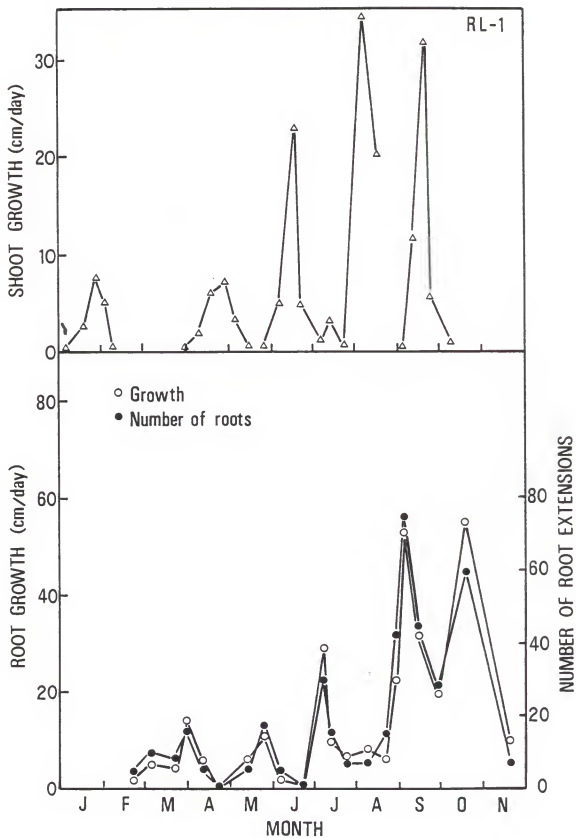


Figure 15. Seasonal changes in root and shoot growth activity in RL-2 during 1982. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.



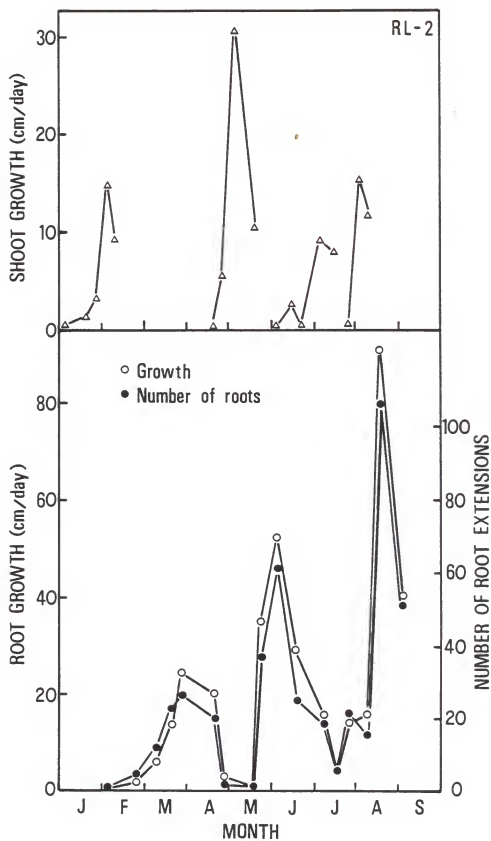


Figure 16. Seasonal changes in root and shoot growth activity in RL-3 during 1982. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.

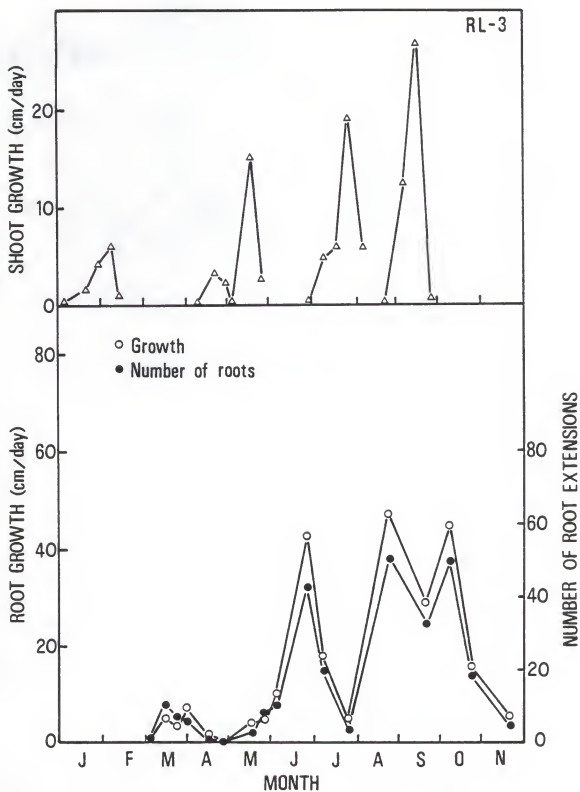


Figure 17. Seasonal changes in root and shoot growth activity in CAR-1 during 1982. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.

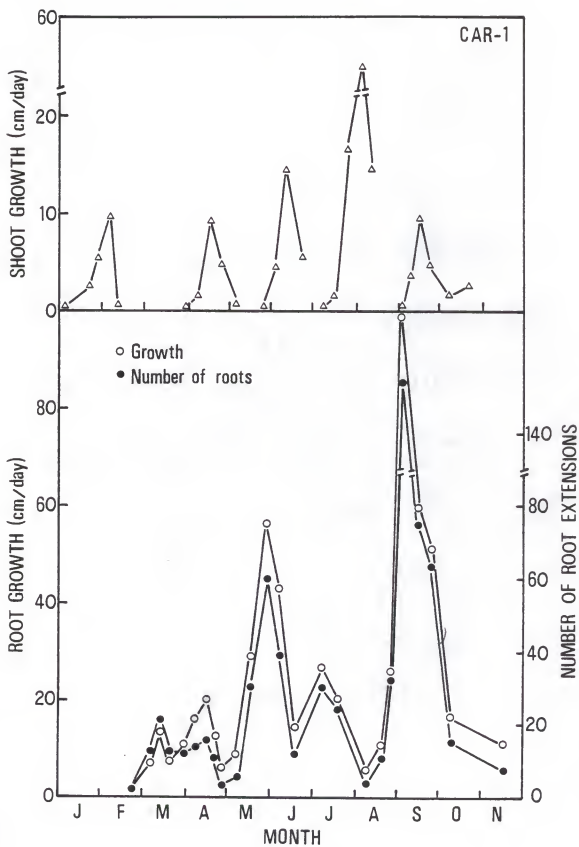


Figure 18. Seasonal changes in root and shoot growth activity in CAR-2 during 1982. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.

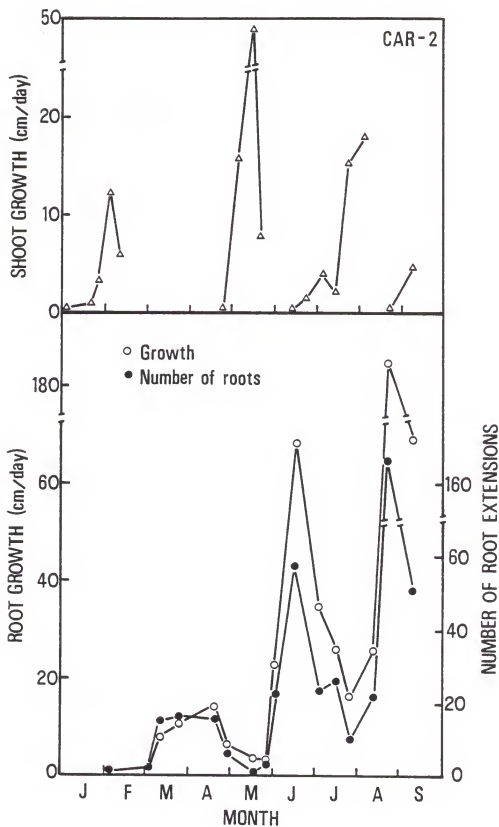
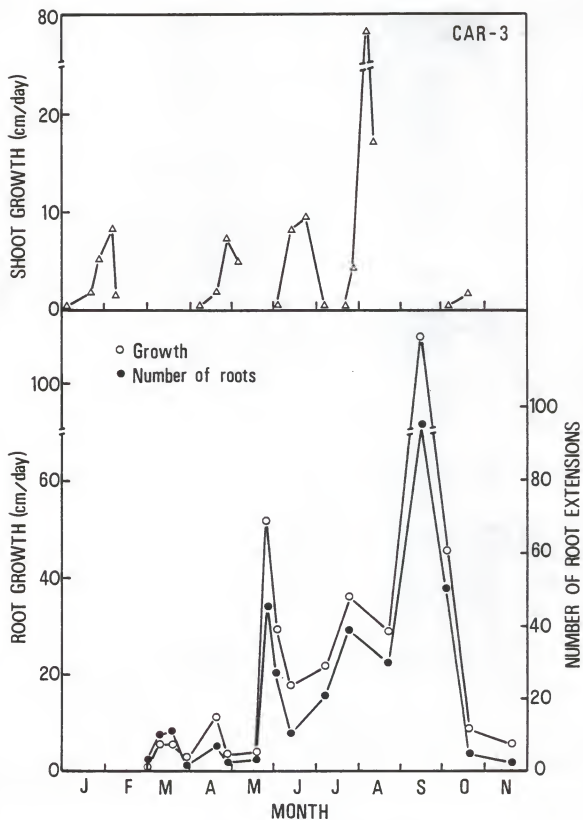


Figure 19. Seasonal changes in root and shoot growth activity in CAR-3 during 1982. Root and shoot growth are expressed as the total increase in length of all visible roots and all shoots between 2 observation dates divided by the number of days in the observation interval. The number of root extensions is the total number of roots which grew between 2 observation dates divided by the number of days in the observation interval.





as 4 weeks. There was no difference between rootstocks in the total length of shoots produced during 1982 (Table 7).

No root growth was observed during January. Root growth resumed in RL-2 (Figure 15) and CAR-2 (Figure 18) in early February, and had resumed in all trees by the end of February. There was a general resumption of growth over the entire visible depth of rooting, which ranged from 90 to 135 cm. Soil temperatures, at the time growth resumed, ranged from 18.8 to 20.0°C (Table 6). The resumption of growth involved the renewed extension growth of existing roots and the development of new lateral roots. Renewed extension growth was observed for both pioneer roots and first order laterals arising from the pioneer roots. New lateral roots were observed to emerge along the entire length of some roots, including regions where considerable secondary thickening had occurred in 1981.

Throughout the year, a close interrelationship was apparent between the pattern of root growth and the pattern of shoot growth. Peak periods of root growth alternated with peak periods of shoot growth (Figures 14 to 19). With the initiation of each shoot growth flush there was a marked decline in root growth activity. Immediately following each shoot growth flush there was a rapid increase in root growth activity which continued until the initiation of the next shoot growth flush. This pattern was evident in all trees.

Table 7. Total length of roots visible at the observation windows and total length of shoots which grew during 1982.

Root-stock	Tree no.	Root length (cm)		Shoot length (cm)	
		Jan-Aug	Jan-Nov	Jan-Aug	Jan-Nov
RL	1	1554	3661	1082	1550
	2	3412	-	987	-
	3	1821	4882	803	1216
	Mean <sup>z</sup>	2262b	4272	957a	1383
CAR	1	3803	6106	1184	1369
	2	5218	-	1094	-
	3	3913	6895	1122	1145
	Mean	4311a	6500	1133a	1257

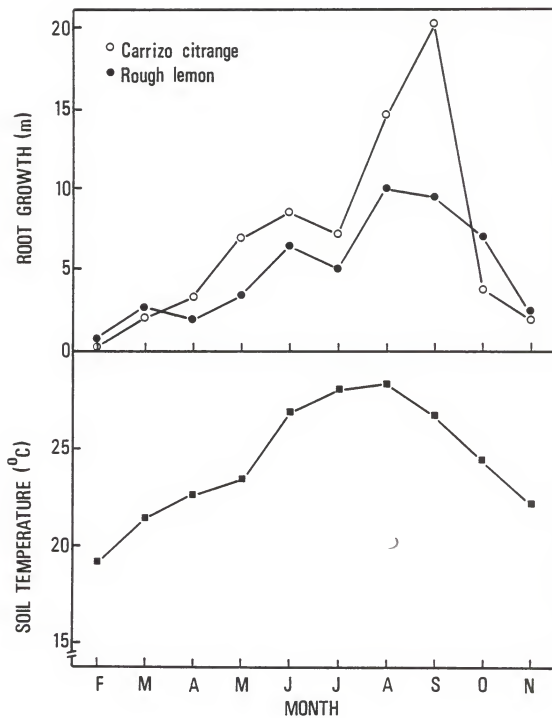
<sup>z</sup>Mean separation within columns by t-test, 5% level.

In spring and early summer, root growth activity declined to very low levels during each period of active shoot growth. The complete cessation of root growth was observed only in RL-3 (Figure 16) in April. During late summer and fall a higher level of root growth activity was generally maintained during shoot growth flushes. This tendency was also observed by Monselise (93) and Waynick and Walker (131).

The close relationship observed in 1981 between extension growth and the number of roots which grew during each observation interval was also apparent throughout 1982 (Figures 14 to 19). During 1982, a significantly greater amount of root growth occurred at the observation windows with Carrizo citrange than rough lemon (Table 7). However, there were no consistent differences between rootstocks in the general pattern of root and shoot growth.

To examine the relationship between the overall seasonal trend in root growth and the seasonal trend in soil temperature, the mean total extension growth for each month was calculated and compared with the mean monthly soil temperature (Figure 20). In both rootstocks, root growth increased with increasing soil temperatures during spring and summer, and decreased with declining soil temperatures after September. Monthly root growth was significantly correlated with mean monthly soil temperature in both rough lemon ( $r = 0.85$ ) and Carrizo citrange ( $r = 0.73$ ).

Figure 20. Mean monthly root extension growth in rough lemon and Carrizo citrange and mean monthly soil temperature in root observation chambers during 1982.



The seasonal pattern of root growth observed in this study differs from the patterns of growth observed in other citrus growing regions of the United States. In studies conducted in Arizona (39), California (131), and north Florida (62), the resumption of root growth in spring occurred in late March or early April, whereas in this study root growth resumed in February. The earlier resumption of root growth in central Florida is apparently a consequence of higher soil temperatures (105). Although soil temperatures were not recorded during December 1981 and January 1982, the long-term studies of DuCharme (42), for the same location, indicate that soil temperatures in central Florida remain above 15°C throughout the year. In contrast, soil temperatures in California remain below the minimum for root growth from December to February (105). In California (131) and Arizona (39), the cessation of root growth in the fall occurred in late October or early November, at least a month earlier than observed here. The longer duration of root growth observed in this study would also appear to be a consequence of higher soil temperatures.

Differences were also apparent in the pattern in growth throughout the year. In the studies conducted in Arizona (39), California (131), and north Florida (62), 3 distinct cycles of active root growth were observed during the year, with both young trees in containers and established field trees. The period of time between growth cycles ranged from 3 to 10 weeks. In this study with young

trees, no prolonged period of inactivity was observed between February and November. More or less continuous root growth throughout the year was also observed in young trees by Marloth (88), under similar climatic conditions in South Africa.

Although the minimum temperature for elongation of citrus roots is approximately  $12^{\circ}\text{C}$  (59, 96), the observations recorded in this study indicate that root growth activity remains limited until much higher temperatures are reached. In greenhouse studies, Cary (25) found that root growth was doubled when the soil temperature was increased from  $19$  to  $25^{\circ}\text{C}$ . Northey et al. (97) observed a similar increase in root growth when soil temperature was increased from  $26$  to  $32^{\circ}\text{C}$ . Under field conditions, Monselise (93) observed that the most intense root growth activity was associated with soil temperatures of  $29^{\circ}\text{C}$  or higher, provided soil moisture was not limiting. Similarly, in this study the most intense root growth activity was observed during the period when soil temperatures were above  $27^{\circ}\text{C}$ . Root growth was limited when soil temperatures were below  $20^{\circ}\text{C}$ .

There have been no previous studies in citrus where seasonal changes in the intensity of both root and shoot growth have been measured quantitatively. The more precise measurements made in this study indicate that with the initiation of each shoot growth flush there is a concomitant decrease in root growth activity. Inconsistencies in the



pattern of alternation which were observed by Marloth (88) were not apparent here. Reduced root growth activity during active shoot growth has also been observed in deciduous fruit trees (67, 68). The alternation of root and shoot growth in fruit trees is attributed to competition between the developing shoots and roots for available assimilates, or to hormonal inhibition as a consequence of elevated auxin levels during active shoot growth (5, 93, 139).

The observed alternation of root and shoot growth activity in citrus indicates that the periods between shoot growth flushes are especially important to the development of the root system. This emphasizes the point that young trees should be well cared for at all times. As the most intense root growth activity occurs during summer, when soil temperatures are above 27°C, particular attention should be paid to the water and nutritional requirements of citrus trees during that period.

### Growth Behavior of Individual Roots

#### Extension Growth Cycles

Individual roots elongated for varying periods of time and underwent repeated cycles of extension growth. Characteristics of the extension growth cycles of pioneer roots, and first and second order fibrous roots are shown in Table 8. These data were compiled from roots whose identity as to type or origin was clearly evident.

Table 8. Characteristics of extension growth cycles of individual roots in relation to rootstock and root type.

Rootstock	Tip diameter (mm)		Duration of growth cycles (days)		Amount of growth per cycle (cm)		No. of cycles per year	Interval between cycles (days)
	Mean	Range	Mean	Range	Mean	Range		
<u>Pioneer</u>								
RL	0.9	0.8-1.1	42	14-71	21.0	11.4-33.6	1-2	28-114
CAR	1.3	0.8-2.1	54	12-264	27.3	4.3-114.3	1-4	12-258
<u>First order fibrous</u>								
RL	0.9	0.8-1.0	18	10-27	11.3	5.1-18.7	1-2	12-24
CAR	1.1	0.8-1.2	30	16-56	14.1	4.5-27.5	1-2	
<u>Second order fibrous</u>								
RL	0.6	0.5-0.6	13	7-22	3.0	1.5-5.6	1-2	11-45
CAR	0.7	0.7-0.8	12	5-37	3.4	1.4-6.6	1-2	

Pioneer roots differed from other root types by undergoing considerable secondary thickening during the course of their development (Figure 21). Individual roots underwent 1 or 2 cycles of extension growth between August and December, 1981, and during 1982 underwent an additional 1 to 4 cycles of extension growth. The duration of growth cycles and the length attained during each cycle were highly variable. Rough lemon roots were observed to elongate for periods of time ranging from 14 to 71 days and Carrizo citrange roots for periods ranging from 12 to 264 days. Short growth cycles were not confined to any particular time of the year. The longest interval observed between growth cycles was 258 days which indicates that individual pioneer roots retain the capacity to renew extension growth for a considerable period of time.

First order fibrous roots (main root of fibrous root bunches) generally elongated for shorter periods of time and made less growth during each growth cycle than pioneer roots. The mean length attained per growth cycle was approximately half the length attained by pioneer roots. The observed duration of growth cycles ranged from 10 to 27 days in rough lemon and from 16 to 56 days in Carrizo citrange. First order fibrous roots were observed to undergo 1 or 2 cycles of growth during 1982.

During the period of this study, second order fibrous roots underwent limited development. These roots were characterized by a smaller tip diameter than first order

Figure 21. Secondary thickened (S) and newly developing (P) pioneer roots at one of the observation windows in CAR-2.



fibrous roots, usually elongated for relatively short periods of time, and did not attain lengths greater than 6 to 7 cm during each growth cycle. These roots were also observed to undergo more than 1 cycle of extension growth, indicating that the capacity to undergo repeated cycles of extension growth is not limited to main roots.

Characteristics of the extension growth cycles of individual roots were generally similar for both rootstocks. However, within each root type, the largest diameter roots occurred in Carrizo citrange, and this was especially noticeable with pioneer roots (Table 8). Apart from the limited observations of Crider (39), no other data are available on the growth behavior of individual citrus roots. Crider (39) also found that individual roots underwent repeated cycles of growth (1 to 3 per year) and elongated for varying periods of time (3 to 45 days). The data reported here show that characteristics of the extension growth cycles of individual roots vary with root type and order of branching. With successive orders of branching, the duration of growth cycles and the length attained during each cycle is diminished.

#### Rate of Elongation

Root elongation rates were determined on roots which grew for the entire period of 1 or more observation intervals. During 1982, the mean elongation rate of Carrizo citrange pioneer roots ranged from 3.4 to 6.2 mm/day (Table

9). The highest rates occurred during summer. The mean elongation rate of first order fibrous roots ranged from 2.3 to 7.0 mm/day, and showed a similar seasonal trend to pioneer roots (Table 10). Less data were available for rough lemon because of the smaller number of roots at the observation windows. Growth rates and seasonal trends appeared to be similar to Carrizo citrange (Tables 9 and 10).

Growth rates of second order fibrous roots were lower than the rates observed for pioneer and first order fibrous roots (Table 11). Mean elongation rates ranged from 1.7 to 3.8 mm/day in Carrizo citrange and from 1.5 to 3.3 mm/day in rough lemon. A reduction in growth rate with progressively higher orders of branching has previously been observed in pecan (140) and red pine (138).

Without reference to root type, Crider (39) reported average rates of elongation for citrus roots ranging from 1.3 to 4.3 mm/day, which are similar to the values observed in this study. Growth rates of citrus roots appear to be generally similar to the rates reported for other fruit trees (10, 71, 110).

The influence of shoot growth on root elongation rates is shown in Figure 22 for CAR-1. The data show that during periods of active shoot growth there is a reduction in root growth rates. This indicates that the decline in extension growth of the root system that is observed during shoot growth involves both a reduction in the number of growing

Table 9. Mean elongation rate of pioneer roots in relation to season and rootstock during 1982.

Month	Mean elongation rate of pioneer roots (mm/day)					
	Rough lemon			Carrizo		
	No. of roots	Mean	SD	No. of roots	Mean	SD
March	4	4.1	0.3	10	3.4	1.5
April	4	6.1	1.2	4	4.5	1.9
May	1	6.6	-	10	4.5	2.1
June				12	4.4	1.5
July	2	6.8	0.5	14	5.0	1.6
August				12	6.2	2.3
September				18	5.4	1.5
October	1	6.1	-	8	4.6	2.6
November	1	3.4	-	2	3.5	0.1



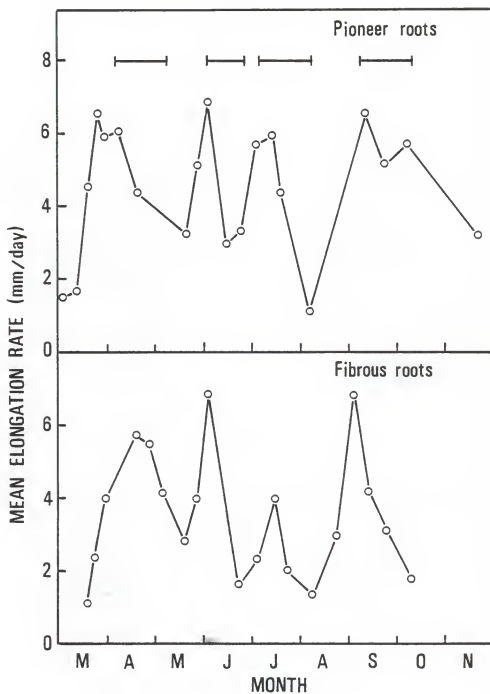
Table 10. Mean elongation rate of first order fibrous roots (main root of fibrous root bunches) in relation to season and rootstock during 1982.

Month	Mean elongation rate of first order fibrous roots (mm/day)					
	Rough lemon			Carrizo		
	No. of roots	Mean	SD	No. of roots	Mean	SD
March	1	3.1	-	8	3.3	1.6
April				10	4.5	1.6
May				9	4.0	1.2
June				12	5.2	1.8
July				3	3.4	1.4
August	9	6.7	4.4	11	7.0	2.3
September	2	4.1	2.5	23	5.0	2.1
October	1	4.6	-	3	2.3	0.8
November				1	4.5	-

Table 11. Mean elongation rate of second order fibrous roots in relation to season and rootstock during 1982.

Month	Mean elongation rate of second order fibrous roots (mm/day)					
	Rough lemon			Carrizo		
	No. of roots	Mean	SD	No. of roots	Mean	SD
March	16	2.3	0.5	6	1.7	0.4
April						
May	3	2.4	0.8	2	1.7	1.3
June	5	1.5	1.4			
July	1	1.6	-			
August	10	3.3	0.8	14	3.8	1.3
September				5	2.1	1.9
October	1	1.7	-			

Figure 22. Influence of shoot growth on the mean elongation rate of pioneer roots and first order lateral roots in CAR-1. Horizontal bars indicate periods of shoot elongation.



roots and a reduction in the growth rate of those roots which continue to elongate during the shoot growth flush.

To determine the relationship between the rate of elongation and soil temperature, the mean elongation rate during specific observation intervals was calculated and compared to the mean soil temperature. As root elongation rates were reduced by the occurrence of shoot growth, only observation intervals in which no active shoot growth occurred were used for this analysis. The data for Carrizo citrange show that there is a linear increase in the rate of elongation with increasing soil temperature (Figure 23). Pioneer and first order fibrous roots showed the same response to temperature.

#### Effect of Water Stress on Root Growth

Water stress was imposed by withholding water from RL-1 and CAR-1 during August. During the period stress was imposed, the mean soil water tension exceeded 0.5 bar in RL-1 (Figure 24) and reached 0.4 bar in CAR-1 (Figure 25). Over the same period, the mean soil water tension in well-watered trees (RL-2 and CAR-2) was maintained below 0.2 bar.

At the beginning of August, root growth activity in all trees was at a relatively low level as a consequence of shoot growth (Figures 24 and 25). In well-watered trees, a marked increase in root growth activity occurred immediately

Figure 23. Relationship between soil temperature and the rate of elongation of pioneer roots and first order lateral roots in Carrizo citrange.

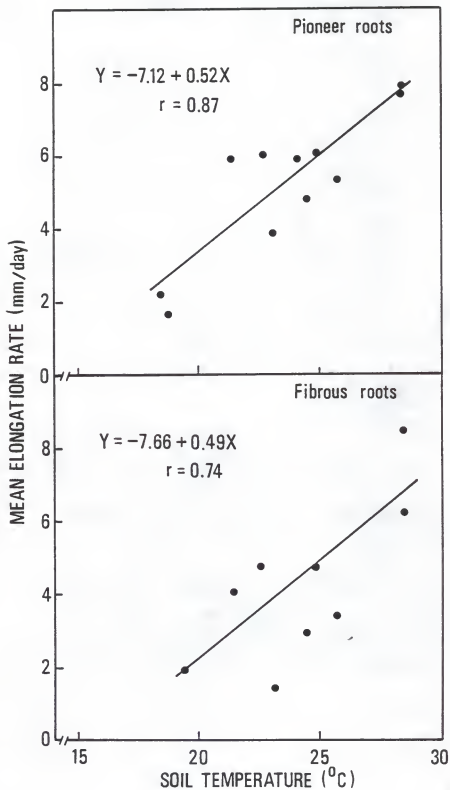


Figure 24. Changes in soil water tension and total extension growth of all visible roots in RL-1 (stressed) and RL-2 (well-watered) during period water stress was imposed. Values for soil water tension are the means of readings at 4 depths. Horizontal bars indicate periods of shoot growth.



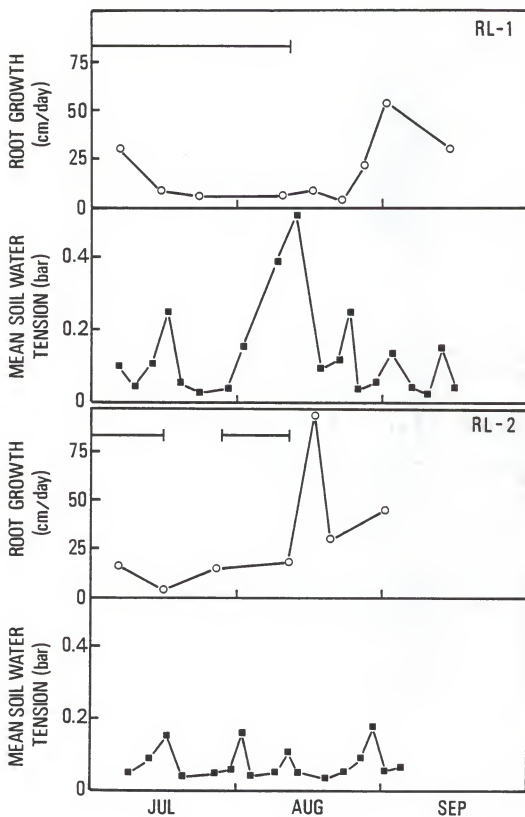
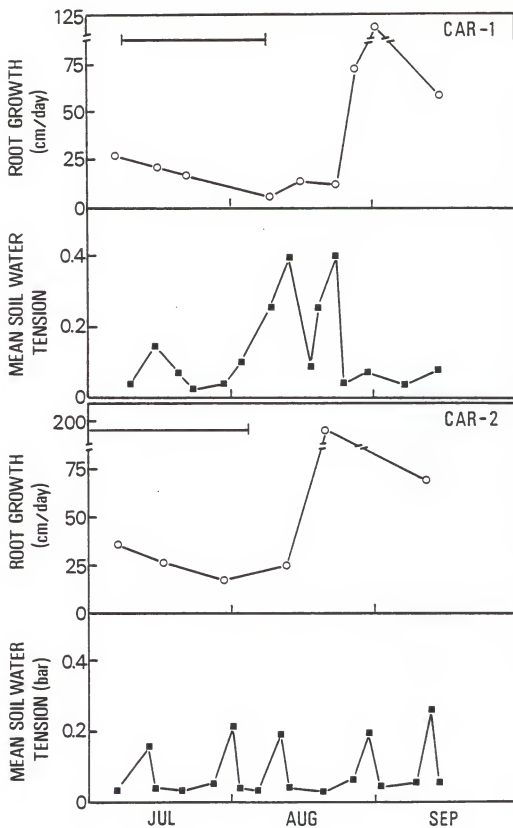


Figure 25. Changes in soil water tension and total extension growth of all visible roots in CAR-1 (stressed) and CAR-2 (well-watered) during period water stress was imposed. Values for soil water tension are the means of readings at 4 depths. Horizontal bars indicate periods of shoot growth.

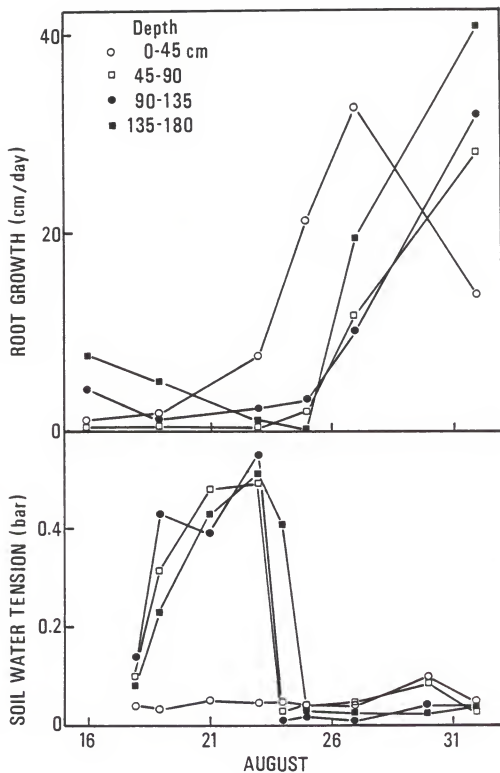


after shoot growth ended in early August. In RL-1 and CAR-1, the level of water stress imposed was sufficient to suppress the marked increase in root growth activity generally observed after the cessation of shoot growth, and root growth activity remained at a low level. No increase in root growth activity was observed until after the entire soil profile was rewetted at the end of the second drying cycle.

During the second drying cycle and the recovery period following rewatering, observations were made at 2 to 4 day intervals to obtain more detailed information on the response to water stress. The pattern of root growth and changes in soil water tension at different depths are shown in Figure 26 for CAR-1. Soil water tension increased rapidly at depths below 45 cm and immediately prior to rewatering was 0.5 bar or higher. At this level of soil water tension very little root growth activity was evident. Root growth activity increased in the surface zone where the soil water tension was less than 0.1 bar. One day prior to rewatering the daytime xylem pressure potential had decreased to  $-24.9 \pm 0.4$  bar, reflecting the dry conditions throughout most of the soil profile. The xylem pressure potential in CAR-2 (well-watered tree) was  $-13.2 \pm 2.8$  bar.

The chamber was irrigated on August 23, and the soil water tension was reduced to less than 0.1 bar at all depths. During the first 2 days after rewatering there was

Figure 26. Changes in soil water tension and total extension growth of all visible roots at different depths in CAR-1 during the second drying cycle and the recovery period after rewatering.



a marked increase in root growth activity in the previously moist surface zone, but there was little change in root growth activity at depths below 45 cm. Two days after rewatering the daytime xylem pressure potential was  $-8.3 \pm 0.6$  bar, which was similar to the well-watered tree ( $-10.3 \pm 1.6$  bar). In the previously dry zones of the profile there was a 2 day lag before any response to rewatering was observed. Between 2 and 4 days after rewatering root growth activity increased markedly at all depths. Changes in total root growth and root elongation rates are shown in Table 12. Although root elongation rates also increased after rewatering, the marked increase in total extension growth was largely due to the increased number of growing roots.

Very little information is available on the levels of soil water stress which begin to restrict root growth in fruit trees. Monselise (93) reported that citrus root growth was very limited at tensions of 7.5 to 8.0 bar, and in sandy soils no root growth was observed at higher tensions. The results from this study indicate that citrus root growth is affected at much lower tensions. In a fine sand soil type, characterized by a very low water holding capacity (Figure 3), root growth activity was clearly checked at soil water tensions near 0.5 bar. This result is similar to Rogers (110) who observed that apple root growth was reduced at tensions of 0.4 to 0.5 bar. The brief periods of stress imposed in this study had no

Table 12. Changes in total root extension growth, the number of roots undergoing extension growth, and the mean elongation rate of individual roots in CAR-1 during the second drying cycle and the recovery period after rewatering.

Observation period	Total root growth (cm/day)	No. of root extensions per day	Rate of elongation (mm/day)
<u>Pre-irrigation</u>			
August 16-19	7.5	12.7	2.1 ± 0.2 <sup>z</sup>
August 19-23	10.2	22.0	2.6 ± 0.4
<u>Post irrigation</u>			
August 23-25	25.9	57.5	4.4 ± 1.0
August 25-27	73.9	143.0	5.6 ± 1.7

<sup>z</sup>Mean ± SD.



obvious effects on the subsequent pattern of root growth after rewatering.

### Morphological Development of the Root System

#### Nursery Trees

The woody framework of the root system of the nursery trees consisted of the taproot and several laterals which generally grew at an oblique angle to the vertically oriented taproot. In all plants the taproot had divided into a number of smaller roots which continued to grow vertically. Although the number of taproots and total length were similar in both rootstocks, the volume, surface area, and dry weight of the taproots were greater in Carrizo citrange (Table 13). Rough lemon had a greater abundance of woody laterals developing from the taproots (Table 13). This observation is consistent with other studies (33, 116).

The total length of fibrous roots exceeded 100 m in both rootstocks and contributed more than 97% of the total length of the root system (Table 13). The fibrous roots were finer in rough lemon than Carrizo citrange. The length/dry weight ratio of the rough lemon fibrous roots was  $3.20 \pm 0.52$  cm/mg, whereas the length/dry weight ratio of the Carrizo citrange roots was  $2.66 \pm 0.39$  cm/mg. The total length, volume, surface area, and dry weight of fibrous roots was greater in Carrizo citrange than rough lemon. In previous studies with Carrizo citrange (33)

Table 13. Total length, volume, surface area, and dry weight of the taproots, woody lateral roots, and fibrous roots of 'Valencia' orange nursery trees on rough lemon and Carrizo citrange rootstocks.

Rootstock	Number	Length (m)	Volume (cm <sup>3</sup> )	Surface area (cm <sup>2</sup> )	Dry weight (g)
<u>Taproots</u>					
Rough lemon	5.1a <sup>z</sup>	1.0a	23.7b	169b	9.4b
Carrizo	5.4a	1.2a	36.0a	229a	13.3a
<u>Lateral roots</u>					
Rough lemon	7.8a	1.6a	6.8a	114a	2.5a
Carrizo	4.6b	1.0a	4.2a	70a	1.5b
<u>Fibrous roots</u>					
Rough lemon	-	103b	30.7b	1989b	3.2b
Carrizo	-	152a	51.6a	3137a	5.7a

<sup>z</sup> Mean separation within columns and root type by t-test, 5% level.

relatively poor fibrous root development was observed near the crown, and it was thought that this was related to the difficulties some growers have experienced in transplanting trees on this rootstock. The greater abundance of fibrous roots observed here indicates that poor fibrous root development near the crown is not an inherent characteristic of Carrizo citrange but something that is apparently related to actual growing conditions in the nursery.

#### Chamber Trees

The entire root systems of RL-2 and CAR-2 were recovered from the chambers 13 months after planting (Figure 27). The diameter and length attained by new roots developing directly from the woody framework of the nursery tree are shown in Table 14. Replacement roots are those roots that developed from the severed ends of the taproots and main laterals (Figure 28). Non-replacement laterals are new main laterals that developed at other sites along the original framework.

Cutting of the taproots and main laterals during digging from the nursery stimulated the development of 1 or more replacement roots from each severed root. As can be seen from the range in length attained by these roots, the pattern of development of individual roots was highly variable (Table 14). Often a single root from the group arising from a particular severed root became dominant and apparently inhibited the development of the remaining roots.

Figure 27. Entire root system of RL-2 displayed on needle board after recovery from root observation chamber.



Table 14. Number, diameter, and length of replacement roots and non-replacement laterals developing from the various components of the original woody framework of nursery tree root system.

Component of nursery tree framework	Root type	Number	Diameter of base (mm)	Length (cm)	
				Mean	Range Total
<u>RL-2</u>					
Taproot	Replacement	13	3.5 ± 1.9 <sup>z</sup>	60	10-166 707
	Non-replacement	12	3.3 ± 1.4	54	12-178 727
First order lateral	Replacement	25	1.9 ± 1.3	41	6-143 961
	Non-replacement	2	2.8 ± 1.2	38	32-43 75
Second order lateral	Replacement	2	1.0	13	4-22 26
	Non-replacement	0			
<u>CAR-2</u>					
Taproot	Replacement	15	3.6 ± 1.3	76	10-149 927
	Non-replacement	19	1.9 ± 0.6	34	4-71 647
First order lateral	Replacement	14	2.4 ± 1.1	42	11-122 549
	Non-replacement	0			
Second order lateral	Replacement	0			
	Non-replacement	1	2.0	-	- 39

<sup>z</sup>Mean  $\pm$  SD.

Figure 28. Replacement roots (R) in CAR-2 which developed from the ends of the taproots and main laterals severed during digging from the field nursery.





In RL-2, 10.3% of the replacement roots attained a length greater than 100 cm, whereas in the CAR-2, 17.2% exceeded this length. Most replacement roots underwent substantial secondary thickening, including those roots that showed very little elongation. Replacement roots retained the same orientation as the parent root. Thus, roots arising from severed taproots continued to grow vertically and were responsible for the rapid vertical development of the root system.

The other major source of roots contributing to the development of the root system framework was new first order laterals arising from the taproots at sites away from the cut ends (Table 14). These roots also showed great variation in their individual development. In RL-2, these non-replacement laterals were similar in the extent of their development to the replacement roots arising from the taproots, and 25% attained a length greater than 100 cm. In CAR-2, non-replacement laterals underwent less growth than the replacement roots and none attained a length of 100 cm. The development of new second order laterals from first order laterals present on the original nursery tree root system made a minor contribution to the development of the root system (Table 14).

Characteristics of the main higher order laterals developing on the replacement roots and first order laterals are summarized in Table 15. At this early stage of development of the root system only a small proportion of these

Table 15. Number, diameter, and length of second order lateral roots developing from replacement roots and first order non-replacement lateral roots.

Type of main axis	Number of laterals	Diameter of base (mm)	Length (cm)		
			Mean	Range	Total
<u>RL-2</u>					
Replacement	10	$1.0 \pm 0.2^z$	33	19-45	347
Non-replacement	5	$1.8 \pm 1.1$	24	10-43	120
<u>CAR-2</u>					
Replacement	90	$1.2 \pm 0.2$	22	3-70	1927
Non-replacement	3	$1.7 \pm 0.3$	27	10-39	80

<sup>z</sup>Mean  $\pm$  SD.

roots had undergone any secondary thickening. However, these roots with their relatively large (1-2 mm) tip diameter and greater length were morphologically distinct from the fine fibrous roots. These roots were especially abundant in CAR-2 and contributed greatly to the developing root system framework. Consequently, the total length of roots comprising the root system framework was greater in CAR-2 than RL-2 (Table 16).

The fine fibrous roots, which were abundant on all components of the root system framework, varied in form from a single axis to roots with up to 3 orders of branching (Figures 29 and 30). The length of the main axis was typically less than 10 cm, but ranged up to 20 cm. The diameter of the subbranches ranged from 0.4 to 0.6 mm. As observed in the nursery trees, the length/dry weight ratio of the fibrous roots was higher in rough lemon ( $3.32 \pm 0.40$  cm/mg) than in Carrizo citrange ( $2.25 \pm 0.22$  cm/mg). The total length, volume, and surface area of fibrous roots was greater in RL-2 (Table 16). However, the total dry weight of fibrous roots was greater in CAR-2. Carrizo citrange fibrous roots were observed to be generally larger in diameter than those of rough lemon. This is reflected in the length/dry weight ratios and explains the greater total dry weight of fibrous roots in CAR-2. The total length of fibrous roots exceeded 3,000 m in both rootstocks and contributed more than 98% of the total length of the root system.

Table 16. Total length, volume, surface area, and dry weight of fibrous roots and roots comprising the root system framework.

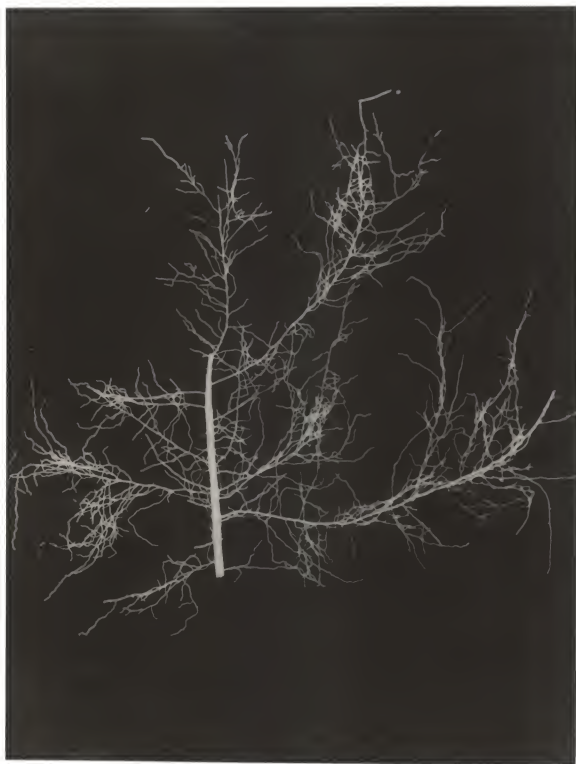
Component of root system	Length (m)	Volume (cm <sup>3</sup> )	Surface area (m <sup>2</sup> )	Dry weight (g)
<u>RL-2</u>				
Framework <sup>z</sup>	31	311	0.30	231
Fibrous roots	3508	751	5.75	106
<u>CAR-2</u>				
Framework	44	301	0.33	201
Fibrous roots	3102	667	5.10	138

<sup>z</sup>Includes original taproots and woody laterals of the nursery tree, replacement roots, and non-replacement laterals.

Figure 29. Part of the root system of CAR-2 displayed on a needle board showing the spatial distribution of fibrous roots.



Figure 30. Fibrous root bunches in RL-2 attached to secondary thickened root of the root system framework.





The above data indicate that the citrus tree root system is capable of undergoing extensive development during the first year after transplanting from the nursery. The long period of the year over which citrus root growth occurs in central Florida (Figures 14 to 19) was no doubt a major factor contributing to this development. Many of the roots responsible for the rapid expansion of the root system originated as replacement roots from the severed ends of the taproots and main laterals of the nursery tree. Root pruning of nursery trees obviously has no adverse effects on the subsequent development of the root system and may actually be of considerable benefit. The stimulation of fast growing, vertically oriented replacement roots from the taproots would rapidly increase the depth of soil from which water could be withdrawn. The development of more than one replacement root from each severed root of the nursery tree would increase the extent of branching of the root system. Greater branching of the root system improves the efficiency with which the soil is exploited.

#### Exposure to Light Study

There were no significant interactions between the light exposure and the observation panel treatments on the number and length of roots of Carrizo citrange seedlings which grew at the observation panel. Continuous exposure to light and exposure for 1 hour per week had no effect on

the number of main roots, but significantly reduced the number of lateral roots that developed (Table 17). The suppression of lateral root development was considerably greater with continuous exposure than exposure for 1 hour per week. Total length of lateral roots was also significantly reduced by exposure to light (Table 17). The type of material used for the observation panel had no effect on the number of roots which grew, but the total length of roots was greater with glass than Plexiglas panels (Table 17). There were no effects of treatment on the elongation rate of main roots (Table 18).

No other data are available on the effect of exposure to light on the growth of citrus roots. In apple, Rogers (111) found that continuous exposure to light suppressed lateral development and that exposure for brief periods of time had considerably less effect. These results are similar to effects observed in this study. Under field conditions, exposure to light during recording is unavoidable. This study with citrus emphasizes that exposure times should be as brief as possible to minimize the suppression of lateral root development. Exposure times in the observation chamber study ranged from 5 to 20 minutes per window, depending on the amount of new root growth. As the extent of suppression of lateral root development depends on the length of exposure, it is likely that the brief periods of exposure to light in the chamber study would have resulted

Table 17. Main effects of light exposure and material used for the observation panel on the number and length of roots which grew at the observation panel.

Treatment	Number of roots			Root length (cm)		
	Main roots	Lateral roots	Total	Main roots	Lateral roots	Total
<u>Light exposure</u>						
Exposed continuously	4.0a <sup>z</sup>	11.8c	15.8c	74.6a	10.5b	85.1a
Exposed 1 hr/week	4.3a	54.0b	58.3b	60.8a	52.9b	113.6a
Not exposed	3.8a	82.3a	86.0a	60.9a	114.4a	175.3a
<u>Observation panel</u>						
Glass	4.7a <sup>y</sup>	47.8a	52.5a	88.2a	73.9a	162.1a
Plexiglas	3.3a	50.8a	54.2a	42.6b	44.7a	87.2b

<sup>z</sup>Mean separation within columns by Duncan's multiple range test, 5% level.

<sup>y</sup>Mean separation within columns by analysis of variance, 5% level.

Table 18. Effect of exposure to light and material used for the observation panel on the rate of elongation of main roots.

Treatment	Elongation rate (mm/day)
<u>Light exposure</u>	
Exposed continuously	4.8 <sup>z</sup>
Exposed 1 hr/week	5.2
<u>Observation panel</u>	
Glass	5.3
Plexiglas	4.7

<sup>z</sup>There were no significant differences between treatments.

in considerably less suppression of root growth than observed here with the 1 hour per week exposure treatment.

## SUMMARY AND CONCLUSIONS

1. The seasonal pattern of root growth of young 'Valencia' orange trees on rough lemon and Carrizo citrange rootstocks was studied in relation to shoot growth, soil temperature, and soil water stress under field conditions in root observation chambers. After 13 months, the entire root systems of 2 trees were recovered from the chambers to study the morphological development of the root system. The effect of exposure to light on root growth was investigated in Carrizo citrange seedlings in root observation boxes.

2. Under the subtropical climatic conditions of central Florida, root growth occurred from February to early December. During the year, the pattern of root growth was closely interrelated with the pattern of shoot growth. Root growth activity declined with the initiation of each shoot growth flush and increased immediately after the cessation of shoot elongation. Thus, a marked alternation of peak periods of root and shoot growth was observed. No differences were apparent between rootstocks in the pattern of root and shoot growth.

3. The overall seasonal trend in root growth was significantly correlated with soil temperature. The most

intense root growth activity occurred during the summer period. Root growth was limited at soil temperatures below 20°C.

4. The number of growing roots and root elongation rates were markedly reduced at a soil water tension of 0.5 bar in fine sand. Brief periods of water stress during summer had no obvious effects on the subsequent pattern of root growth after rewatering.

5. Individual roots were observed to undergo cycles of extension growth. The duration of growth cycles and root elongation rates varied with root type and order of branching. In Carrizo citrange, the mean duration of extension growth cycles ranged from 12 days in second order fibrous roots to 54 days in pioneer roots. During the year, the mean elongation rate of pioneer roots ranged from 3.4 to 6.2 mm/day and was highest during summer. The mean elongation rate of second order fibrous roots ranged from 1.7 to 3.8 mm/day. Characteristics of the growth behavior of individual roots were similar in both rootstocks.

6. A detailed study of the morphological development of the root system showed that many of the roots responsible for the rapid expansion of the root system originated as replacement roots. These roots developed from the ends of taproots and main laterals severed during digging from the nursery. Root pruning of nursery trees apparently has no adverse effects on the subsequent development of the root system and may actually be of considerable benefit.

The development of more than one replacement root from each severed root of the nursery tree increases the extent of branching of the root system and thereby increases the effectiveness with which the soil is exploited.

7. Measurement of total root length showed that the citrus tree root system is capable of undergoing extensive development during the first year after transplanting from the nursery. The total length of fibrous roots increased from 100-150 m to more than 3,000 m in both rootstocks. Fibrous roots comprised more than 98% of the total length of the root system.

8. Continuous exposure to light suppressed the development of lateral roots. Exposure for 1 hour/week also reduced lateral root development but had considerably less effect than continuous exposure. This emphasizes that exposure times should be kept to a minimum during recording of root growth.



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He is married to the former Janet Fisher, and they have two children, Kylie and Sharlene.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

William S Castle  
William S. Castle, Chairman  
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Horticultural Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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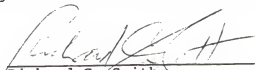
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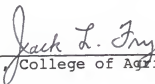
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